

THE APLACOPHORAN FAMILY PROCHAETODERMATIDAE IN THE  
NORTH AMERICAN BASIN, INCLUDING *CHEVRODERMA* N.G. AND  
*SPATHODERMA* N.G. (MOLLUSCA; CHAETODERMOMORPHA)\*

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ABSTRACT

Six species in three genera of Prochaetodermatidae are described from over 650 stations and 5200 specimens in the Atlantic and north Pacific Oceans from depths between 500 and 7300 m. Included are all species in the North American Basin and all species in *Chevroderma* n.g.

Three principal characters differentiate prochaetodermatid species and genera: spicules, radula, and body shape. Family membership is defined by radula and jaws, spicule morphology determines genus, and species are described by spicules and radula. Mean body shape describes populations of species. Interference colors produced by the aragonite spicules indicate spicule thickness and symmetry. The variation in *Prochaetoderma yongei* n. sp., described in detail, establishes the taxonomic base on which to judge the morphological limits of a prochaetodermatid species.

*Spathoderma* n.g. and *Chevroderma* n.g. differ from each other and from the genus *Prochaetoderma* in spicule morphology. *P. yongei* and *S. clenchi* n. sp. are widespread northwestern and eastern Atlantic continental slope and abyssal rise species. *C. turnerae* and *C. gauson* n. spp. are abyssal species, the former occurring throughout the Atlantic, the latter only in the northern West European Basin. *C. scalpellum* n. sp. is a slope species of restricted range in the eastern Atlantic. *C. whitlatchi* n. sp. is a wide-ranging abyssal and hadal species of the northern east and mid-Pacific. A wide geographic range is correlated with a vertical depth distribution greater than 1500 m.

All species are patchy in distribution but particular species can be numerically dominant and occur at high densities locally, e.g., up to 400 m<sup>-2</sup> for *P. yongei* and 178 m<sup>-2</sup> for *C. whitlatchi*. In the north Atlantic, greatest numerical abundances and lowest diversity of Prochaetodermatidae occur in the North American Basin.

INTRODUCTION

Aplacophoran mollusks belonging to the family Prochaetodermatidae are the most numerous and widespread of the Chaetodermomorpha in the deep sea. They have been taken at all depths in the north and south Atlantic Ocean, Mediterranean Sea, central, north and east Pacific Ocean, and in the western Pacific off southeastern Australia (unpub. data). Particular species are sometimes numerically among the most abundant macrofaunal species in quantitative samples and are thus an important part of the deep-sea fauna (Scheltema, 1981).

Previously the family has consisted of only two named species belonging to the genus *Prochaetoderma*: *P. raduliferum* (Kowalevsky 1901) from the Mediterranean and *P. californicum* Schwabl 1963 from the troughs off southern California, although other unnamed species have been figured (Treece, 1979, Fig. 5; Scheltema, 1978, Figs.

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1A, 2, 3B; 1981, Figs. 1D, 2E-G, 3D-H, K, 7, 11A-C). Collections taken in the last two decades from both the Atlantic and Pacific Ocean contain several new species and genera belonging to this family.

Six new species in three genera are described here, including all the species that occur in the North American Basin and all those so far collected that belong to the new genus *Chevroderma*. The variation in one species, which has a broad geographic range, is described in detail to establish the taxonomic base on which to judge the morphological limits of a species in the family Prochaetodermatidae.

#### MATERIALS AND METHODS

Descriptions are based on examination of more than 5200 specimens from the Atlantic Ocean and 68 from the Pacific including the following regions (Tables I, II; Fig. 1): in the Atlantic west of the Mid-Atlantic Ridge—North American Basin, Newfoundland Basin, Brazil Basin, and Argentine Basin; in the Atlantic east of the Mid-Atlantic Ridge—West European Basin, Canary Basin, Cape Verde Basin, Angola Basin, and Namibia Basin; in the eastern Pacific—Panama Basin, Galapagos vents area, off southern California, off Oregon, and Aleutian Trench; and in the mid-Pacific—just north of the Equator.

Samples were taken with a variety of quantitative and nonquantitative gear. The latter included several types of trawls and epibenthic sleds, and the former, box and tube corers manipulated from submersibles and box corers and anchor dredges put overboard (see footnote, Table I).

Most samples were screened using a flotation method (Sanders *et al.*, 1965), fixed in formaldehyde, and preserved in 70–80% alcohol on shipboard. Samples were later sorted into taxa in the laboratory.

Measurements of specimens were made by using dividers or a digitizer on lines drawn length- and crosswise on camera-lucida images at 12× or 25×. Measurements were made to the nearest 0.01 mm in the first two species described, with an accuracy of 0.05 mm; however, it was found that the precision of measurements is not greater than 0.1 mm, and all subsequent measurements are so given.

Treatment of spicules for both light transmission and scanning electron microscopy and of radulae has been previously described (A. Scheltema, 1972, 1976). Permanent preparations of spicules and radulae were made by drying them directly on a slide and mounting with a standard histological plastic medium. Spicules were also examined under cross-polarized light to measure thickness. X-ray diffraction showed them to be formed of aragonite with the long axes of the crystals parallel to the long axis of the spicule, and by comparing the highest interference color with a standard crystallographer's chart, greatest thickness was estimated to the nearest 0.5 μm. Selected isochromes were drawn to show the pattern of thickening and symmetry of the spicules (see Fig. 2C). Length and width of spicules were measured with an ocular micrometer.

Length and width of radula teeth, central plates, and jaws (shown in Fig. 15) were measured with an ocular micrometer.

#### TYPE MATERIAL

Types are deposited in the National Museum of Natural History, Washington, DC (USNM) and the Muséum National d'Histoire Naturelle, Paris (MNHN). Each holotype is preserved in buffered 80% alcohol after removing a few spicules to a permanent slide. Specimens from the type locality and those used for illustrating spicules

TABLE I  
*Specimens examined. Atlantic Ocean (Prochaetoderma yongei, Spathoderma clenchi, Chevroderma turnerae, C. gauson, and C. scalpellum)*

Cruise or dive no.*	Station	Gear**	Date	Depth m	Latitude	Longitude	<i>P. yongei</i>	<i>S. clenchi</i>	<i>C. turnerae</i>	<i>C. gauson</i>	<i>C. scalpellum</i>
					North American Basin						
					North	West					
ATLANTIS 263 or 264	E #3	AD	25/V/61	823	39°50.5'	70°35'	5				
	F #1	AD	24/V/61	1500	39°47'	70°45'	7				
	G #1	AD	24/V/63	2000	39°42'	70°39'	3	1			
	II #2	AD	24/V/61	3752	38°05'	69°36'			1		
ATLANTIS 298	58	AD	7/IX/63	2000	38°34.3'	72°55.0'	3	1			
ATLANTIS II-12	61	AD	20/VIII/64	2000	39°43.3'	70°37.8'	5	2			
	62	ES	21/VIII/64	2496	39°26'	70°33'		5			
	70	ES	23/VIII/64	4680	36°23'	67°58'			6		
	73***	ES	25/VIII/64	1470	39°46.5'	70°43.3'	911***	19			
CHAIN-50	81	ES	2/VII/65	5042	39°41'	66°28'	?1				
	84	ES	4/VIII/65	4749	36°24.4'	67°56'			15		
	85	ES	5/VII/65	3834	37°59.2'	69°26.2'			6		
	87	ES	6/VII/65	1102	39°48.7'	70°40.8'	986				
ATLANTIS II-17	92	ES	13/XII/65	4694	36°20'	67°56'			3		
	95	ES	17/XII/65	3753	38°33'	68°32'			4		
CHAIN-58	103	ES	4/V/66	2022	39°43.6'	70°37.4'	7	18			
	104	AD	4/V/66	2050	39°41.3'	70°35.9'		1			
	105	ES	5/V/66	530	39°56.6'	71°03.6'	1				
ATLANTIS II-24	115	ES	16/VIII/66	2030	39°39.2'	70°24.5'	175	211			2
	120	ES	20/VIII/66	5018	34°43.0'	66°32.8'					6
	121	ES	21/VIII/66	4800	35°50.0'	65°11.0'					12***
	122***	ES	21/VIII/66	4833	35°50.0'	64°57.5'					4
	125	ES	23/VIII/66	4825	37°24.0'	65°54.0'					4
	126	ES	24/VIII/66	3806	39°37.0'	66°47.0'					4
ATLANTIS II-30	128	ES	16/XII/66	1254	39°46.5'	70°45.2'	45				
	131***	ES	18/XII/66	2178	39°38.5'	70°36.5'	21	71***			?1
ATLANTIS II-40	175	ES	29/XI/67	4667	36°36'	68°29'					13
	178	AD	1/XII/67	1839	39°44.8'	70°32.0'	3	5			
CHAIN-88	207	ES	21/II/69	805	39°51.3'	70°54.3'	166				

209	ES	22/II/69	1501	39°47.6'	70°49.9'	435	6		
210	ES	22/II/69	2024	39°43.0'	70°46.0'	78	274		
352	SBC	11/VII/76	3600	38°16.5'	69°38.5'			2	
367	SBC	19/VII/76	1764	39°45.5'	70°37.2'	48	11		
370	SBC	19/VII/76	1815	39°44.9'	70°35.0'	20†	3†		
340	ES	24/XI/73	3264	38°14.4'	70°20.3'		1	1	
346	ES	3/XII/73	457	39°54.1'	70°10.7'	3			
Core 1	SBC	IV/80	4617	40°21.5'	63°06.2'			1	
ALVIN-328:									
407-2; 08-18,									
19; 436-2; 437-									
7; 459-6, 11,									
12, 15, 16;									
460-3, 4, 7, 16;									
546-3; 773-A;									
774-4; 776-2,									
3, 4; 794-2;									
834-2									
ALVIN-603-2, 3									
ALVIN-1311									
Mud Box 2-80									
DOS #2	Exp.	36 mo.	3644	38°18.4'	69°35.6'			2	
DWD	BEB	28/VII/75-2/ VIII/75	1833- 2452	38°45'- 38°57'	72°06'- 72°34'	14	33		
Newfoundland Basin									
HA	BEB	26/VI/72-13/ IX/72	1141- 1800	39°20'- 39°28'	72°03'- 72°13'	9	8		
HCR	BEB	15/VIII/75	3264	38°46'	71°10'		1		
RAD	BEB	3/VIII/76	2749	38°30'	72°11'		1		
334	ES	30/VIII/72	4400	40°42.6'	46°13.6'			14	
Brazil Basin									
South									
155	ES	13/II/67	3730	00°03.0'	27°48.0'			2	
156	ES	14/II/67	3459	00°46.0'	29°28.0'			11	
ATLANTIS II-31									



TABLE I (Continued)

Cruise or dive no.*	Station	Gear**	Date	Depth m	Latitude	Longitude	<i>P. yongei</i>	<i>S. clenchi</i>	<i>C. turnerae</i>	<i>C. gausson</i>	<i>C. scalpellum</i>
					Argentine Basin						
					South						
						West					
ATLANTIS II-60	242	ES	13/III/71	4382	38°16.9'	51°56.1'			5		
	243	ES	14/III/71	3815	37°36.8'	52°23.6'			1		
	245	ES	14/III/71	2707	36°55.7'	53°01.4'			74		
	246	ES	15/III/71	3343	37°15.1'	52°45.0'			2		
	247	ES	17/III/71	5208	43°33.0'	48°58.1'			4		
	259	ES	26/III/71	3305	37°13.3'	52°45.0'			13		
	262	ES	27/III/71	2440	36°05.2'	52°17.9'			13		
					West European Basin						
					North						
						West					
CHAIN-106	313	ES	17/VIII/72	1500	51°32.2'	12°35.9'	19				
	321	ES	20/VIII/72	2890	50°12.3'	13°35.8'		1			
	323	ES	21/VIII/72	3356	50°08.3'	13°53.7'		10			
	326	ES	22/VIII/72	3859	50°04.9'	14°23.8'			6		
	328	ES	23/VIII/72	4426	50°04.7'	15°44.8'			11		
	330***	ES	24/VIII/72	4632	50°43.5'	17°51.7'			13		
	DS-01	ES	15/VII/76	2091	57°59.7'	10°39.8'	2	141		8	
	DS-02	ES	16/VII/76	2081	57°58.8'	10°48.5'	1	23		8***	
	CP-01	CP	16/VII/76	2040	57°57.7'	10°55.0'		13			
	CP-02	CP	16/VII/76	2091	57°58.4'	10°42.8'		2			
	CP-03	CP	17/VII/76	2466	56°38.0'	11°06.4'		1			
	CP-04	CP	17/VII/76	2483	56°33.2'	11°11.3'		2			
	DS-05	ES	18/VII/76	2503	56°28.1'	11°11.7'		172			
	DS-06	ES	18/VII/76	2494	56°26.6'	11°10.5'		215			
	DS-07	ES	19/VII/76	2884	55°00.7'	12°31.0'		3			
	DS-08	ES	19/VII/76	2891	55°02.0'	12°34.6'		55			
	CP-05	CP	19/VII/76	2884	55°00.4'	12°29.4'		22			
	CP-06	CP	19/VII/76	2888	55°02.3'	12°40.3'		6			
	DS-09	ES	20/VII/76	2897	55°07.7'	12°52.6'		74			1



TABLE I (Continued)

Cruise or dive no.*	Station	Gear**	Date	Depth m	Latitude	Longitude	<i>P. yongei</i>	<i>S. elenchi</i>	<i>C. turnerae</i>	<i>C. gausson</i>	<i>C. scapellum</i>
	DS-61	ES	25/II/74	2250	47°34.7'	8°38.8'		3			
	DS-62	ES	26/II/74	2175	47°32.8'	8°40'		1			
	DS-63	ES	26/II/74	2126	47°32.8'	8°35'		1			
	DS-64	ES	26/II/74	2156	47°29.2'	8°30.7'		2			
	KR-33	KR	24/II/74	2963	47°30.4'	9°06.9'			1		
	KR-35	KR	25/II/74	4140	47°26'	9°08.7'			1		
BIOGAS-V	DS-66	ES	16/VI/74	3480	47°28.2'	9°—			6		
	DS-67	ES	17/VI/74	4150	47°31'	9°35'			5		
	DS-70	ES	21/VI/74	2150	44°08.8'	4°17.4'		2			
BIOGAS-VI	DS-77	ES	24/X/74	4240	47°31.8'	9°34.6'			1		
	DS-78	ES	25/X/74	4706	46°31.2'	10°23.8'			5		
	DS-79	ES	26/X/74	4715	46°30.4'	10°27.1'			6		
	DS-80	ES	27/X/74	4720	46°29.5'	10°29.5'			4		
	DS-82	ES	29/X/74	4462	44°25.4'	4°52.8'			1		
	DS-85	ES	30/X/74	4462	44°23.2'	4°50.8'			6		
	DS-86	ES	31/X/74	1950	44°04.8'	4°18.7'	8				
	DS-87	ES	1/XI/74	1913	44°05.2'	4°19.4'	6		2		
	DS-88	ES	1/XI/74	1894	44°05.2'	4°15.7'	1				
	CP-14	CP	23/X/74	4237	47°32'	9°35.9'			10		
	CP-15	CP	25/X/74	4715	46°32.2'	10°28.5'			4		
	CP-16	CP	25/X/74	4825	46°27.3'	10°25.8'			1		
	CP-17	CP	26/X/74	4706	46°30.8'	10°19.5'			2		
	CP-19	CP	28/X/74	4434	44°24.9'	4°51.3'			3		
	CP-20	CP	29/X/74	4459	44°23.2'	4°51.4'			2		
	CP-22	CP	30/X/74	4475	44°22.9'	4°54.8'			8		
	CP-22A	CP	30/X/74	4475	44°22.9'	4°54.8'			1		
	CP-25A	CP	1/XI/74	1894	44°05'	4°17'	1				
BIOGAS-VIII	KG-142	SBC	18/IV/79	2182	47°33.4'	8°39.7'		1			
	KG-144	SBC	to	2225	47°34.2'	8°40.3'		1			
	KG-145	SBC	8/VI/79	2170	47°32.9'	8°39.1'		2			
	KG-157	SBC		2227	47°34.3'	8°39.8'		1			
	KG-173	SBC		2740	47°31.6'	9°04.2'		1			
BIOGAS-IX	KG-174	SBC	16/IV/80	2885	47°32.5'	9°05.5'		1			
	KG-178	SBC	17/IV/80	2885	47°32.5'	9°05.5'		1			
	KG-179	SBC	18/IV/80	2770	47°32.1'	9°05.2'		1			
	KG-179	SBC	18/IV/80	2730	47°32.2'	9°04.5'		1			

BIOGAS XI	KG-181	SBC	18/IV/80	2811	47°31.5'	9°06.4'	2				
	KG-183	SBC	18/IV/80	2748	47°31.5'	9°05.1'	1				
	KG-185	SBC	19/IV/80	2828	47°32.0'	9°06.3'	1				
	KG-183	SBC	18/IV/80	2748	47°31.5'	9°05.1'	1				
	KG-185	SBC	19/IV/80	2828	47°32.0'	9°06.3'	1				
	KG-203	SBC	4/X/81	4210	47°34.9'	9°39.8'		2			
	KG-206	SBC	4/X/81	4130	47°35.2'	9°39.5'		1			
	KG-207	SBC	4/X/81	4135	47°35.3'	9°38.5'		6			
	KG-208	SBC	4/X/81	4130	47°35.0'	9°40.0'		4			
	KG-209	SBC	6/X/81	4190	47°34.4'	9°38.9'		3			
	KG-210	SBC	7/X/81	4135	47°35.4'	9°39.2'		2			
	KG-211	SBC	7/X/81	4170	47°34.7'	9°39.1'		4			
	KG-212	SBC	7/X/81	4130	47°34.9'	9°39.3'		1			
	KG-213	SBC	7/X/81	4150	47°34.7'	9°39.0'		2			
	KG-215	SBC	7/X/81	4110	47°34.8'	9°39.9'		3			
	KG-216	SBC	7/X/81	4200	47°35.0'	9°38.5'		1			
	KG-218	SBC	8/X/81	4170	47°34.8'	9°40.3'		1			
	MAC 81	Exp.	11 mo.	2120	47°33.4'	8°33.7'		1			
	SARSIA	65	ES	25/VII/67	1922	46°15'	4°50'		1		
	DISCOVERY	6710	ES	19/III/68	2670	27°23.6'	15°39.6'		4		
6711		ES	19/III/68	2988	27°14.9'	15°36.3'		1			
ATLANTIS II-31	142	ES	5/II/67	1624	10°30.0'	17°51.5'		11			
	145	ES	6/II/67	2185	10°36.0'	17°49.0'		9			
ATLANTIS II-42	195	ES	19/IV/68	3797	14°49'	9°56'		5			
	198	ES	21/IV/68	4559	10°29'	9°04'		1			
	199	ES	22/IV/68	3764	9°47'	10°29'		4			

## Canary Basin

## West

## North

## Cape Verde Basin

## West

## North

## Angola Basin

## East

## South

TABLE I (Continued)

Cruise or dive no.*	Station	Gear**	Date	Depth m	Latitude	Longitude	<i>P. yongei</i>	<i>S. clenchi</i>	<i>C. turnerae</i>	<i>C. gausson</i>	<i>C. scalpellum</i>
	200	ES	22/V/68	2644	9°41'	10°55'		4			1
	201	ES	22/V/68	1964	9°29'	11°34'					22
	202***	ES	23/V/68	1427	9°05'	12°17'	3				59***
WALDA	DS-18	ES	22/VII/71	4079	6°37.5'	8°18.2'			4		
					Namibia Basin						
					South	East					
ATLANTIS II-42	191	ES	17/V/68	1546	23°05'	12°31.5'	66				
	194	ES	17/V/68	2864	22°54'	11°55'		5			
WALDA	DS-04	ES	9/VI/71	4184	21°57.5'	9°22.7'			6		
	DS-08	ES	22/VI/71	3777	21°58.6'	10°16'			3		
TOTAL SPECIMENS							3122	1480	538	19	102

\* Woods Hole Oceanographic Institution cruises: ATLANTIS, ATLANTIS II, CHAIN, KNORR, OCEANUS; Woods Hole Oceanographic Institution dives: ALVIN; Centre National de Tri d'Océanographie Biologique (Brest) cruises: INCAL, NORATLANTE, THALASSA, BIOGAS, MAC, WALDA; National Institute of Oceanography (U.K.) cruises: SARSIA, DISCOVERY.

\*\* Quantitative gear, lowered on wire from shipboard: AD—anchor dredge (0.40–1.00 m<sup>2</sup>), SBC—spade box corer (0.25 m<sup>2</sup>), KR—Reineck corer (600 cm<sup>2</sup>); manipulated from submersible: BEB—Birge-Ekman box corer (25 m<sup>2</sup>, 44.5 m<sup>-2</sup>), TC—tube corer (35 cm<sup>2</sup>), BC—box corer (22.5 cm<sup>2</sup>), BC—box corer (22.5 cm<sup>2</sup>), Nonquantitative samplers: ES—epibenthic sled trawl, CP—perch trawl, WS—Wormley trawl, GBS, PBS—large, small Boillot sled trawls. Experimental boxes: Exp.

\*\*\* Type locality.

† Only inner 90 cm<sup>2</sup> of box core sorted.

TABLE II

*Material examined, Pacific Ocean (Chevroderma whitlatchi)*

Cruise or dive no.*	Station or core	Gear**	Date	Depth m	Latitude north	Longitude west	No.
Aleutian Trench							
SEVENTOW Leg 7	H-39	SBC	20/VII/70	7298	50°58.0'	171°37.5'	31
Off Oregon							
Oregon State U.	AD-136	AD	9/II/65	2800	44°50.9'	127°34.1'	1
Off Baja California							
MELVILLE 70- III-I	n.d.	n.d.	21/III/70	3950	31°47.0'	120°14.8'	1
Panama Basin							
ALVIN 1132, 1230-32, 1234-39	***	BC	9/IX/81- 14/VI/ 82	3912	5°20.7'	81°56.2'	31***
Near Galapagos Vents							
GILLISS-301	Core 14	SBC	18/II/79	2730	00°35.0'	86°05.7'	1
Mid-Pacific							
DOMES Proj.	48-22	SBC	n.d.	5117	8°16.0'	151°11.3'	2
	53-45	SBC	n.d.	4985	11°43.9'	138°22.2'	1

\* Scripps Institution of Oceanography cruises: SEVENTOW, MELVILLE 70; Woods Hole Oceanographic Institution dives: ALVIN; Galapagos Biology Expedition cruise: GILLISS; U.S. National Oceanographic and Atmospheric Administration project: DOMES.

\*\* See footnote, Table I.

\*\*\* Type locality.

and radulae are designated as paratypes; for most illustrated paratypes there are permanent slides of spicules and radulae.

#### TAXONOMIC CHARACTERS

The taxonomy of the Aplacophora has in the past relied primarily on interpretation of histological sections, and most species descriptions have been based on one or a few specimens. The results have not made for easily accessible or recognizable characters for purposes of identification. Radulae and spicules have seldom been adequately figured, and no studies exist that rigorously describe intraspecific variation within a species.

The acquisition of large deep-sea benthic samples over wide geographic areas since the early 1960s has made numerous specimens available for studying aplacophoran species both between and within populations. The insights gained from these large and numerous samples have shown that for the Prochaetodermatidae, hard parts and



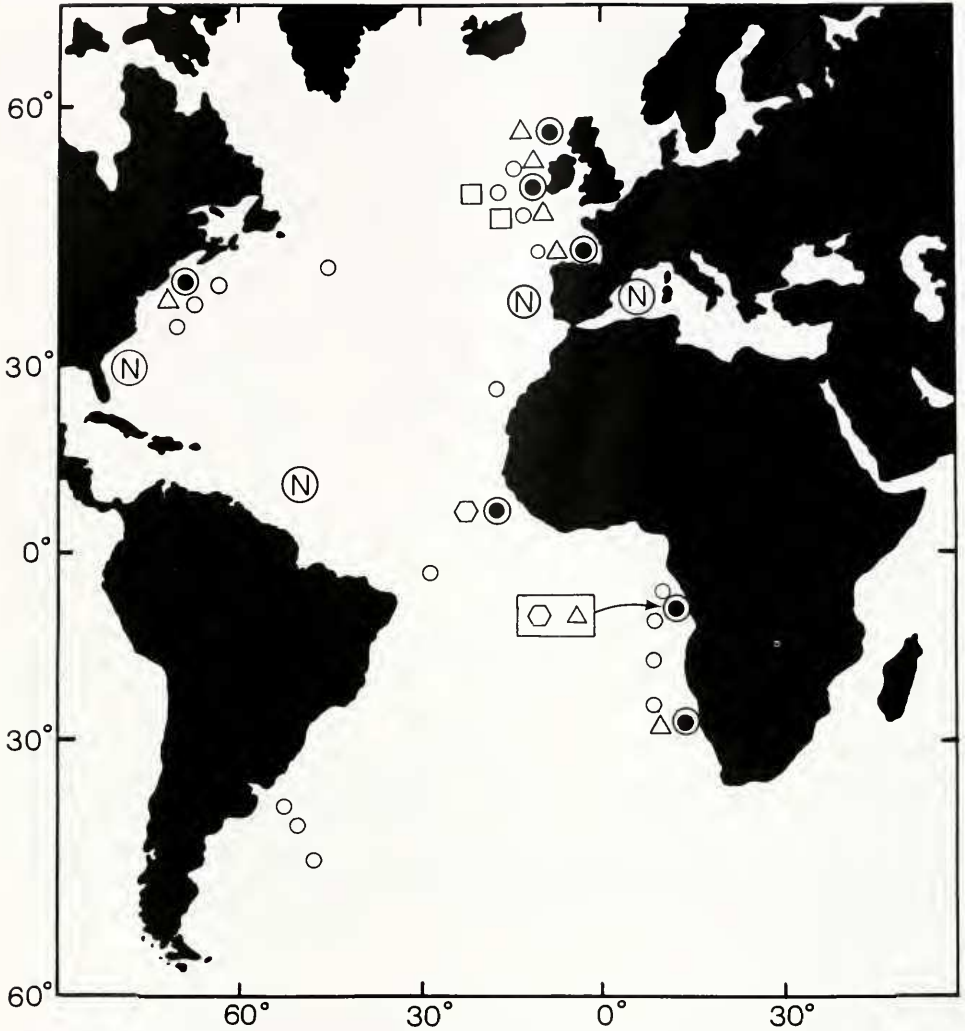


FIGURE 1. Distribution of *Prochaetoderma yongei* (solid, ringed circle), *Spathoderma clenchi* (triangle), *Chevroderma turnerae* (open circle), *C. gaussoni* (square), and *C. scalpellum* (hexagon). Data generalized from about 165 stations listed in Table I. Circled N, area sampled in which none of the five species occurred.

external morphologies characterize species, and that the morphology of spicules determines affinities and defines genera in this family.

No internal soft anatomy has been used here to describe species because of the great histologic similarity among species and because the size and arrangement of internal organs is reflected in the body shape.

#### *Body shape*

The body of the Prochaetodermatidae is cylindrical and divided into three regions: anterium, trunk, and posterium (Fig. 2A). The *anterium* bears the oral shield and few

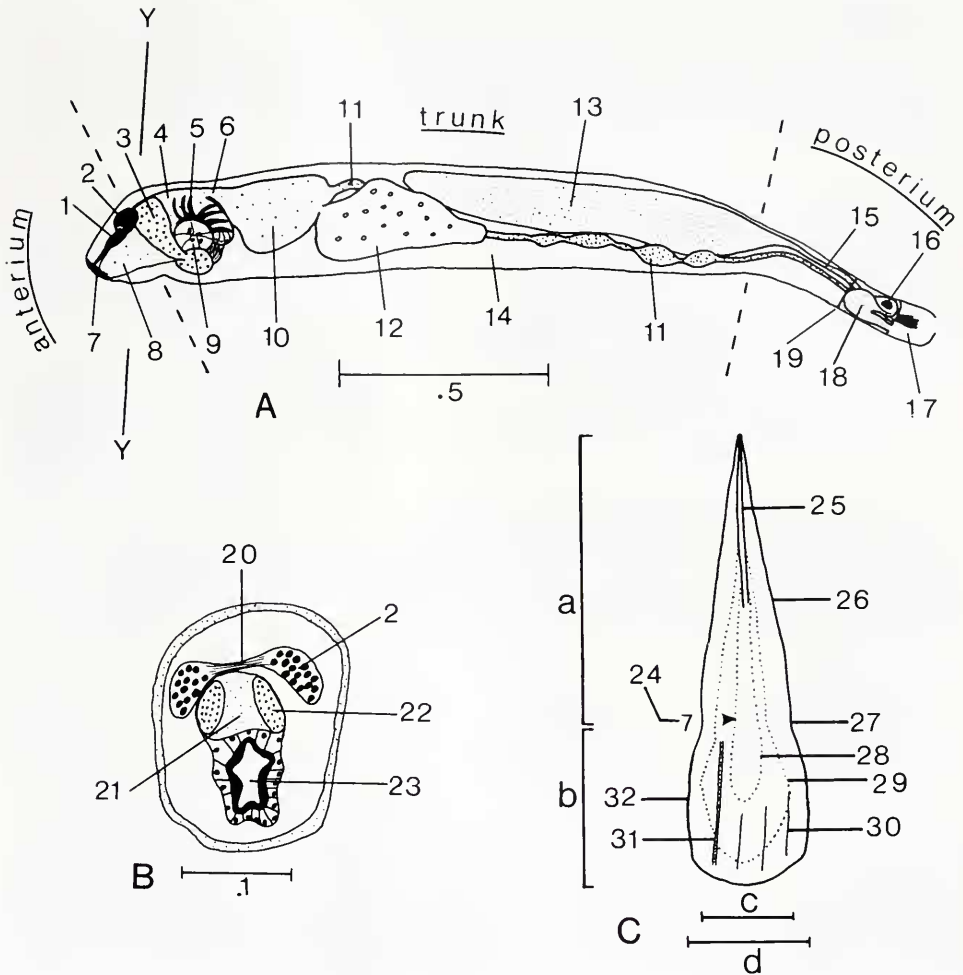


FIGURE 2. A. Genus *Prochaetoderma*, generalized anatomy, semi-diagrammatic. Dashed lines indicate boundaries between body regions. B. Cross-section through Y-Y in diagram A showing distal ends of jaws and separated lobes of cerebral ganglia joined by thick commissure. C. Morphological characters of a spicule. 1 precerebral ganglion, 2 cerebral ganglion, 3 jaw, 4 buccal cavity, 5 radula, 6 esophagus, 7 oral shield, 8 oral cavity, 9 chondroid-like bolster, 10 stomach, 11 intestine, 12 digestive gland, 13 gonad, 14 hemocoel, 15 gonopericardial duct, 16 heart within pericardium, 17 cloaca or mantle cavity with gill, 18 coelomduct, 19 vertical posterior septum, 20 cerebral commissure, 21 sheet of cuticle joining distal ends of jaw, 22 distal end of jaw, 23 cuticle-lined oral cavity, 24 greatest spicule thickness in micrometers indicated by arrowhead and numeral, 25 keel or heavy ridge, 26 blade edge, 27 waist, 28 and 29 isochromes, 30 fine ridge, 31 groove, 32 base edge, *a* blade length, *b* base length, *c* maximum blade width, *d* maximum base width.

spicules and is often inflated; it may be retracted and introverted in preserved specimens. The *trunk* is set off from the anterium by a much greater density of spicules. The *posterium* is narrower than the trunk and often elongate and tail-like; the exact demarcation between trunk and posterium is sometimes difficult to establish.

Measurements of the trunk and posterium allow quantification of the variation in body shape among populations of a single species, as well as differentiating body shape among species.

### Oral shield

The paired oral shield varies in size among species of Prochaetodermatidae (Fig. 3); size is also related to specimen size within a species and thus must be used cautiously as a taxonomic character. The relative sizes among species can be compared quanti-

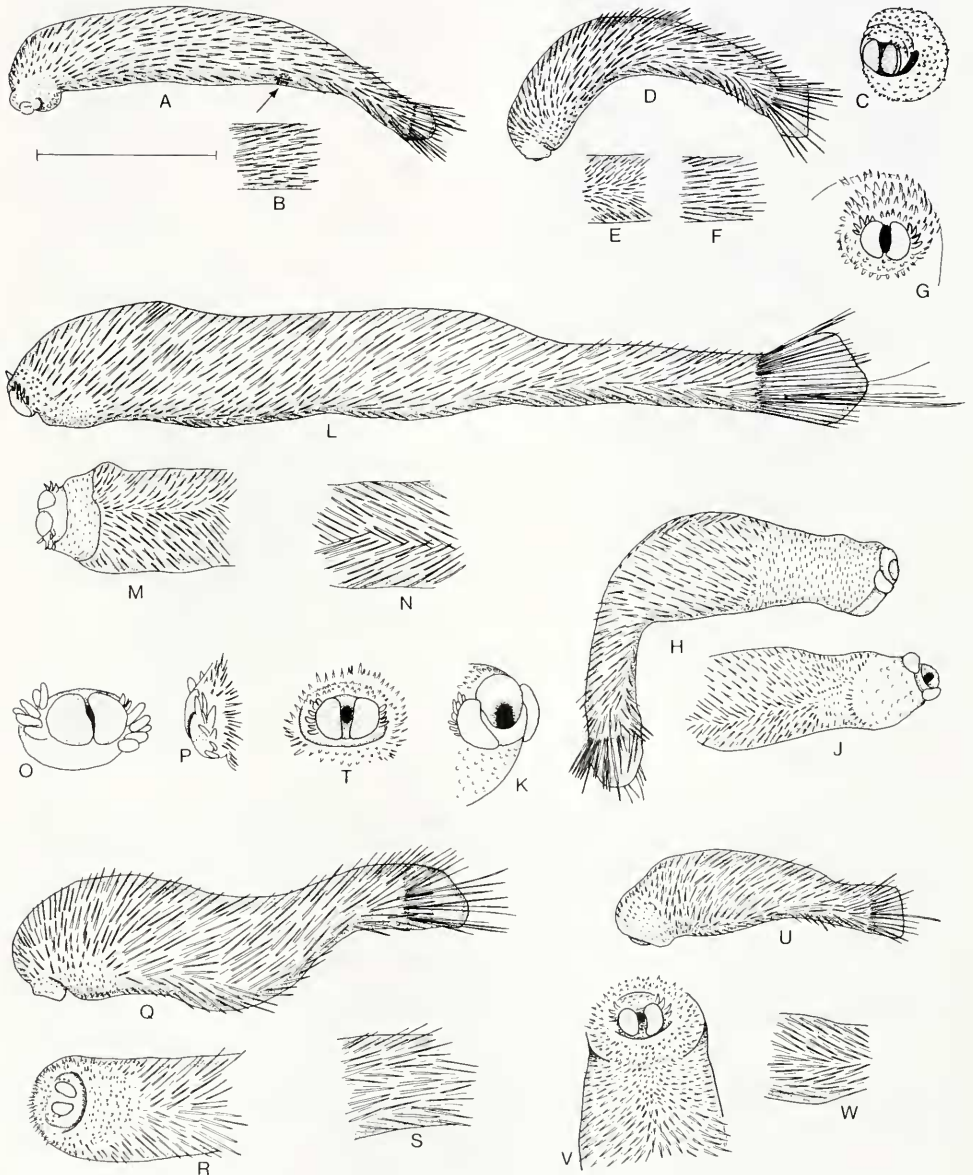


FIGURE 3. Holotypes. A-C. *Prochaetoderma yongei* n. sp. D-G. *Spathoderma clenchi* n.g. n. sp. H-K. *Chevroderma whittlatchi* n.g. n. sp. L-P. *Chevroderma turnerae* n. sp., genus type. Q-T. *Chevroderma gausson*, n. sp. U-W. *Chevroderma scalpellum* n. sp. Distribution of spicules, mid-dorsal view: B, F, N, S, W; mid-ventral view: E, M, J, R, V. Scale line equals 0.5 mm for oral shield illustrations C, G, K, O, P, T, and V; for all remaining illustrations it equals 1.0 mm.

tatively by using the following index:  $(\text{length} \times \text{width of oral shield}) \div (\text{trunk diameter}) \times 100$ . This index is given for holotypes.

There may be relatively large, possibly tactile oral-shield spicules just lateral to the oral shield (Figs. 3G, K, O, P); they are lacking or indistinct in some species (Fig. 3C).

#### *Cloaca, or mantle cavity*

The posterior end of the body is rounded or truncated in lateral view, the shape depending on the cloacal wall musculature which closes off the mantle cavity (Fig. 3).

#### *Spicules*

*Attitude.* According to species, spicules are carried flat against the body or bent outwards from it. They may be arranged with the long axis parallel to the body axis (Fig. 3A) or obliquely with the proximal end ventral to the distal end (Fig. 3L). A species may be translucent or opaque according to spicule thickness and attitude. The morphology of the spicules and body wall musculature determine the attitude of spicules relative to the body wall.

*Morphology.* The morphology of individual spicules is the taxonomic character most useful for distinguishing species and for determining relationships among species. A spicule has a *base* (Fig. 2C), which lies within the cuticle and is anterior in position to the *blade*, which is external to the cuticle; the base is usually set off from the blade by a *waist*. The blade may have a *keel* on the frontal surface; *ridges* or *grooves* may be present on either the blade or base. Spicules may be symmetrical or asymmetrical. Symmetry is revealed by interference colors seen under cross-polarized light. Spicules may lie flat in one plane, or the blade may be rotated about the long axis to a plane different from that of the base or it may be bent at the waist towards the body or away from it.

Spicules vary in their morphology both along the body from anterior to posterior and from the ventral to the lateral and dorsal sides; thus they are here described from particular regions of the body, which are indicated on a drawing of the specimen from which the spicules were taken (Figs. 6–13). However, dorsal spicules at the junction of the trunk and posterium are usually adequate for species determination and their morphology alone is given under the diagnosis for each species.

#### *Radula and jaws*

The jaws and radula of the family Prochaetodermatidae have been described by Kowalevsky (1901) and Scheltema (1981). There is great morphological similarity among species in these structures, the greatest differences lying in size of jaws and teeth and in shape and length of the central plate (Figs. 14, 15). No statistically significant correlations were found in mature specimens of two species (a) between specimen length and either tooth or jaw length, or (b) between tooth length and jaw length. The ranges in ratios of tooth length to jaw length are similar in all six species described here.

The jaws can usually be seen *in situ* within a specimen viewed with transmitted light and thus family membership determined without dissection.

### SYSTEMATIC ACCOUNT

#### Family Prochaetodermatidae Salvini-Plawen 1969

The Prochaetodermatidae are Chaetodermomorpha (= Caudofoveata), or burrowing, footless solenogasters, uniquely characterized by the presence of a pair of



large, cuticular jaws and the morphology of a small distichous radula. The cuticle of the jaws is discrete from the buccal cavity cuticle (Scheltema, 1981); it is bound by basement membrane and not produced by preradular, lateral pouches as stated in Boss (1982). The radula is formed of 8 to 12 rows of paired teeth on an undivided radular membrane; between each pair is a central plate. A lateral, tooth-like projection of the radular membrane lies alongside each tooth (Fig. 15 upper left tooth; Scheltema, 1981, Figs. 7D, 11A). Each tooth has a lateral membranous "wing" and a membranous median extension, or brush, bearing many serrations (Figs. 4E, 15). The distal teeth are worn (Scheltema, 1981, Fig. 11B). The odontophore bolsters are chondroid-like (Fig. 2A; Scheltema, 1978, Fig. 3B).

All prochaetodermatid species are small, usually less than 5 mm in body length, and thicker anteriorly than posteriorly. Although the body is cylindrical, the dorsal and ventral surfaces are distinct: the spicules diverge away from the ventral midline and the body of contracted specimens is usually flexed into an arch, the dorsal side uppermost. The oral shield is divided into two lateral parts with or without lateral spicules. The epidermal spicules are solid, with ornamentation simple or lacking; the base is flat in cross-section and embedded in the epidermal cuticle; the blade is flat, oval, or triangular to round in cross-section and extends beyond the cuticle. Paired groups of long, lateroventral spines trail posteriorly beyond the cloaca (Figs. 3L, U) but are often broken off in preserved specimens.

Three distinct body regions reflect internal anatomy (Fig. 2A): (1) the anterior is a hemocoelic space surrounding an expansible oral cavity into which can be protruded the jaws and buccal mass (Fig. 10, specimen); (2) a broad trunk, with weak body-wall musculature, contains the paired lobes of the cerebral ganglion with their thick commissure (Fig. 2B), buccal mass, stomach, digestive gland, anterior intestine, and gonad; and (3) a narrow posterium, with strong longitudinal muscles, contains the posterior intestine, unpaired gonoduct (paired in other chaetodermatids), heart, pericardium, paired coelomoducts, and, posteriorly, a small cloaca with a pair of gills, each formed of two lamellae (Salvini-Plawen, 1969, Fig. 12). The stomach is unique among the Chaetodermomorpha in lacking a dorsal ciliated typhlosole, and it has no locally thickened cuticle; the digestive gland is uniquely without a dorsal band of granular cells (Scheltema, 1981). The members of the family are dioecious; in translucent species, sex can often be determined without dissection.

Except in the Scandinavian fjords, Arctic, and Antarctic where they have not been reported, the Prochaetodermatidae are ubiquitous in soft oceanic sediments from 50 to over 7000 m.

#### Genus *Prochaetoderma* Thiele

*Prochaetoderma* Thiele 1902, *Zeit. Wiss. Zool.* **72**: 275.

With characters of the family. Spicules flat; base shorter than blade, blade broad and triangular with median keel and sharp distal point.

Distribution: Atlantic Ocean and Mediterranean Sea, 50–2000 m.

Type species: *Chaetoderma radulifera* Kowalevsky 1901, by monotypy; Sea of Marmara.

#### *Prochaetoderma raduliferum* (Kowalevsky)

*Chaetoderma radulifera* Kowalevsky 1901, *Arch. Zool. Exp.*, ser. 3, **9**: 264–274, Figs. 1–20. Sea of Marmara, Isle des Princes, 35–40 fms. [Type specimen unknown; type figure, here designated, P1. 10, Fig. 3; redrawn herein, Fig. 6].

*Prochaetoderma raduliferum*. Salvini-Plawen, 1972, pp. 37–39, Figs. 10–12 in *Fifth European Marine Biology Symposium*, B. Battaglia, ed. Piccin Editore, Padova.

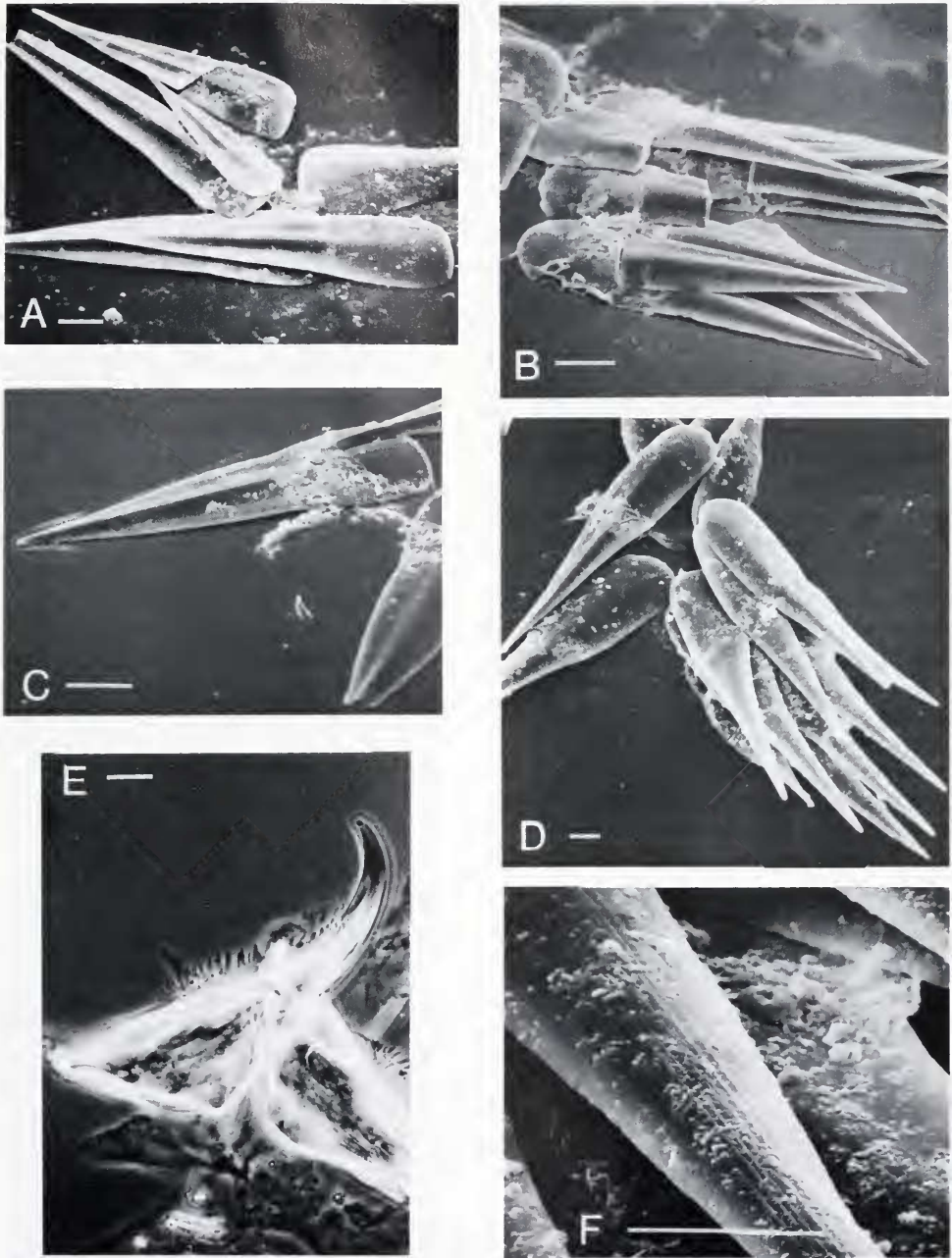


FIGURE 4. Spicules of *Prochaetoderma yongei* n. sp. (A–C) and *Spathoderma clenchi* n.g., n. sp. (D, F); radula tooth (E) of an unnamed species of Prochaetodermatidae. A. *P. yongei* holotype, 1470 m, North American Basin (cf. Fig. 6); B. *P. yongei*, 805 m, North American Basin (CH-88 Sta. 207) (cf. Fig. 7); C. *P. yongei*, 1546 m, Namibia Basin (All-42 Sta. 191) (cf. Fig. 8); D. *S. clenchi* holotype, 2178 m, North American Basin (cf. Fig. 9); F. same as D, detail of blade. Scale lines equal 20  $\mu$ m.



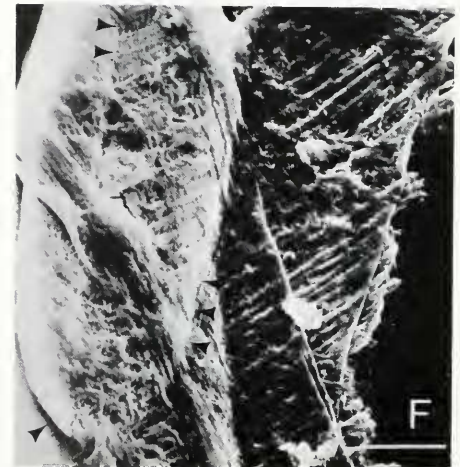
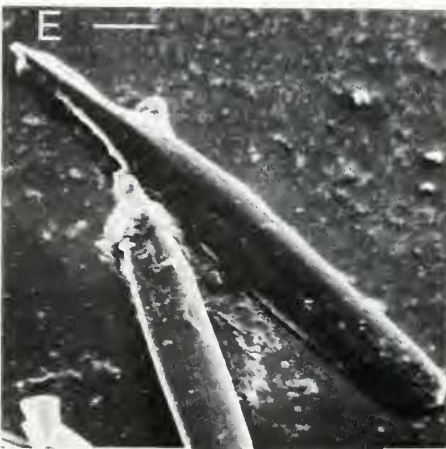
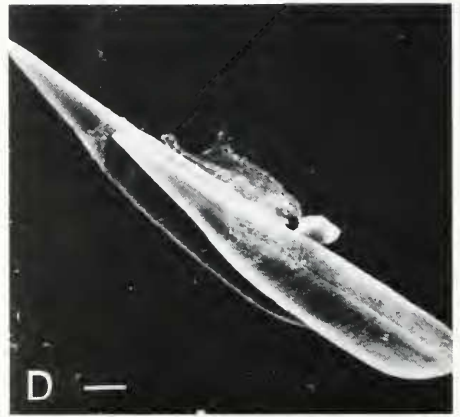
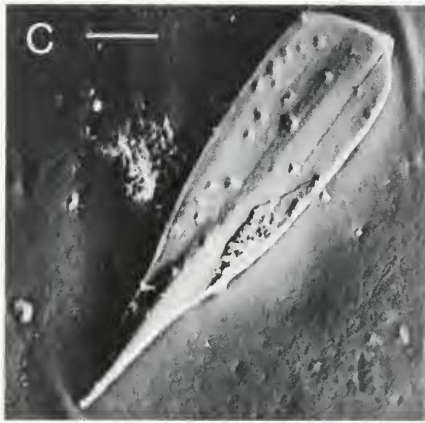
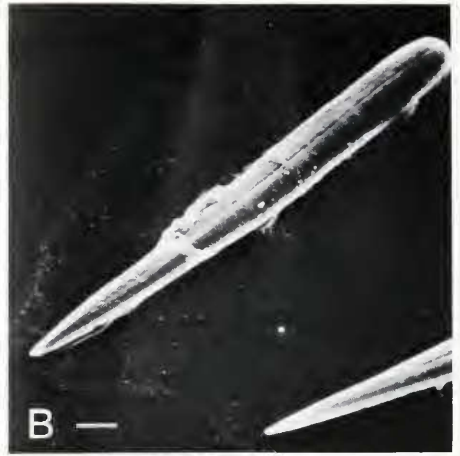


FIGURE 5. Spicules of four species of *Chevroderma* n.g. A. *C. gauson*, paratype no. 5, 4829 m, West European Basin (cf. Fig. 11); B. *C. turnerae*, holotype, 4,833 m, North American Basin (cf. Fig. 10); C. *C. scalpellum*, paratype no. 1, 1427 m, Angola Basin (cf. Fig. 12); D. *C. turnerae*, paratype no. 5, 4237 m, West European Basin (cf. Fig. 10 W spicule 4); E. *C. whitlatchi*, paratype no. 2, 7298 m, Aleutian Trench (cf. Fig. 13); F. *C. turnerae*, paratype no. 5, showing spicule embedded in crossed fibers of cuticle, arrowheads point to edge of spicule and longitudinal groove. Scale lines equal 20  $\mu$ m.

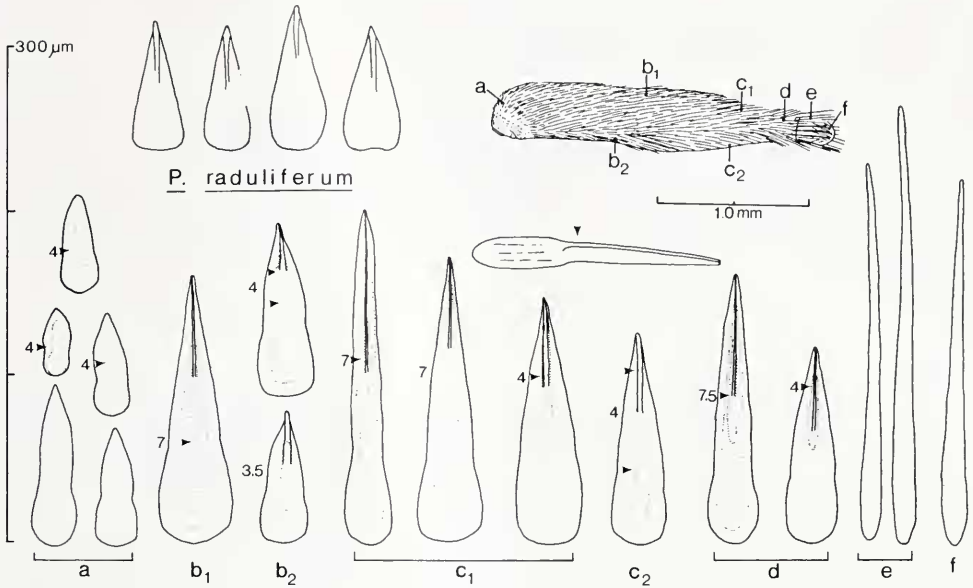


FIGURE 6. Upper left: spicules of *Prochaetoderma raduliferum* (Kowalevsky 1901) redrawn from type figure (pl. 10, Fig. 3); scale of original drawings not certain, scale used here from Salvini-Plawen (1972, Fig. 12 d, f). Lower rows: spicules of *Prochaetoderma yongei* n. sp. paratype no. 1, 1470 m, North American Basin (type locality). Spicules a-f from body regions indicated on figured specimen, above right; spicule below specimen, lateral view of a trunk spicule showing blade slightly offset outwards from base (arrowhead).

*Prochaetoderma raduliferum*. Salvini-Plawen, 1977, *Vie Milieu* 27: 56–63, Figs. 3–5; *Bull. Mus. Nat. Hist. Nat., Paris* (ser. 3), 447 (Zool. 310): 417, Table 1.

Distribution: Sea of Marmara; eastern and western Mediterranean; 54–2415 m.

*Prochaetoderma yongei* n. sp.

Figs. 1, 3A–C, 4A–C, 6, 7, 8, 14 y<sup>1</sup>–y<sup>3</sup>; Tables I, III, IV, V, VII

*Prochaetoderma* sp. Grassle, 1977, *Nature* 265: 618–619, Table 2.

*Prochaetoderma* sp. Scheltema, 1978, *Malacologia* 17, Figs. 1A, 3B, 5C.

*Prochaetoderma* sp. y. Scheltema, 1981, *Malacologia* 20, Figs. 2E–G, 3D–H, K, 7D–F, 11A–C (non 7A–C, caption in error).

*Prochaetoderma* sp. B. Scheltema, 1985, in L. Laubier and C. Monniot, eds., *Peuplements Profonds du Golfe de Gascogne: Campagnes BIOGAS, IFREMER, Brest*, pp. 391–396, Tables 1, 2.

**Diagnosis:** Translucent, slender; spicules flat-lying, parallel to long axis of body; less than 3 mm long, posterium  $\frac{1}{4}$  total length; posteroventral thickened cuticular patch present; oral shield small, oral shield spicules not distinct; spicules straight, sharply keeled, indented at waist, blade with convex sides, base flared proximally, greatest length 252  $\mu$ m; greatest jaw length 365  $\mu$ m; radula tooth length up to 90  $\mu$ m; central radula plate short and relatively broad with ends directed posteriorly, greatest length 26  $\mu$ m.

This species is named in honor of Sir Maurice Yonge, whose book *The Seashore* early led me to the study of marine animals.

Holotype: North American Basin, 39°46.5'N, 70°43.3'W, 1470–1330 m (ATLANTIS II-12, Sta. 73, 25/VIII/64). USNM No. 850201.

Illustrated paratypes:

Nos. 1, 4: Type locality, USNM Nos. 850202 (No. 1), 850208 (No. 4).

No. 2: Namibia Basin, 23°05'S, 12°31.5'E, 1546–1559 m (ATLANTIS II-42 Sta. 191, 17/V/68). USNM No. 850204.

No. 3: North American Basin, 39°51.3'N, 70°54.3'W, 805–811 m (CHAIN-88 Sta. 207, 21/II/69). USNM No. 850206.

### Description

*External morphology.* *Prochaetoderma yongei* is a small, slender, translucent species with flat-lying spicules oriented anterior-posterior except where they diverge along the ventral midline (Fig. 3A, B). Oral shield spicules are indistinct. The total body length averages 1.5 to 2.1 mm in seven populations; the greatest length is 2.8 mm. Trunk diameter averages 0.3 to 0.4 mm, with greatest diameter 0.6 mm. The posterium is about ¼ total length; it averages 0.4 to 0.5 mm in length and 0.2 mm in diameter and ranges up to 1.0 mm by 0.3 mm. The mean index of posterium length to trunk length averages 0.31 to 0.35 in seven populations, but the range is great, from 0.18 to 0.68. An opaque, thickened patch of cuticle at the ventral junction of the trunk and posterium is characteristic of the species (Fig. 3A, arrow). The oral shield is small (Fig. 3C); the cloaca is rounded.

Holotype: Male; total length 2.6 mm; trunk 2.0 by 0.4 mm; posterium 0.6 by 0.2 mm; index of posterium to trunk 0.30. Oral shield 0.05 by 0.09 mm; index of oral shield to trunk diameter 1.12.

*Spicules.* A median keel runs the length of the blade; it is sharpest and most distinct distally (Figs. 4A–C, 6, 7, 8) and is lacking in anteriormost and posteriormost spicules from regions *a*, *e*, and *f*. Other ornamentation on the blade is lacking except in region *b*<sub>1</sub> from specimens in the Namibia Basin, which have short ridges parallel to the keel (Fig. 8). The spicule base is flared proximally with convex sides and sometimes faint ridges; occasionally the base has straight sides which are either flared or parallel. The proximal end is usually rounded, but may be straight or broadly triangular. The blade usually has convex sides proximally; it is distinctly set off from the base by an indentation at the waist. Some blades have straight sides, particularly in juveniles (Fig. 7D). Distally the sides of the blade straighten or become slightly concave before tapering to a sharp point. The isochromes are symmetrical. Spicules from the anterior end of the body are thickest at the proximal part of the blade just above the waist (region *b*<sub>1</sub>); further posteriorly, they are thickest more distally (regions *c* and *d*). In lateral view the base and blade are nearly straight, with the blade somewhat offset outwards from the base and slightly bent towards the body. Spicules from the ventral side of the body are thinner and shorter than those from the lateral and dorsal sides, and often the keel extends like a needle beyond the sides of the blade (regions *b*<sub>2</sub>, *c*<sub>2</sub>). Very short, very thin (2 µm) triangular spicules occur sparsely.

Ranges in dimensions of spicules from region *c* for eight populations in five ocean basins are shown in Table III.

The spicules of *P. yongei* differ from those figured by Kowalevsky (1901) for *P. raduliferum* in having a longer blade and a distinct waist (Fig. 6). The sides of the

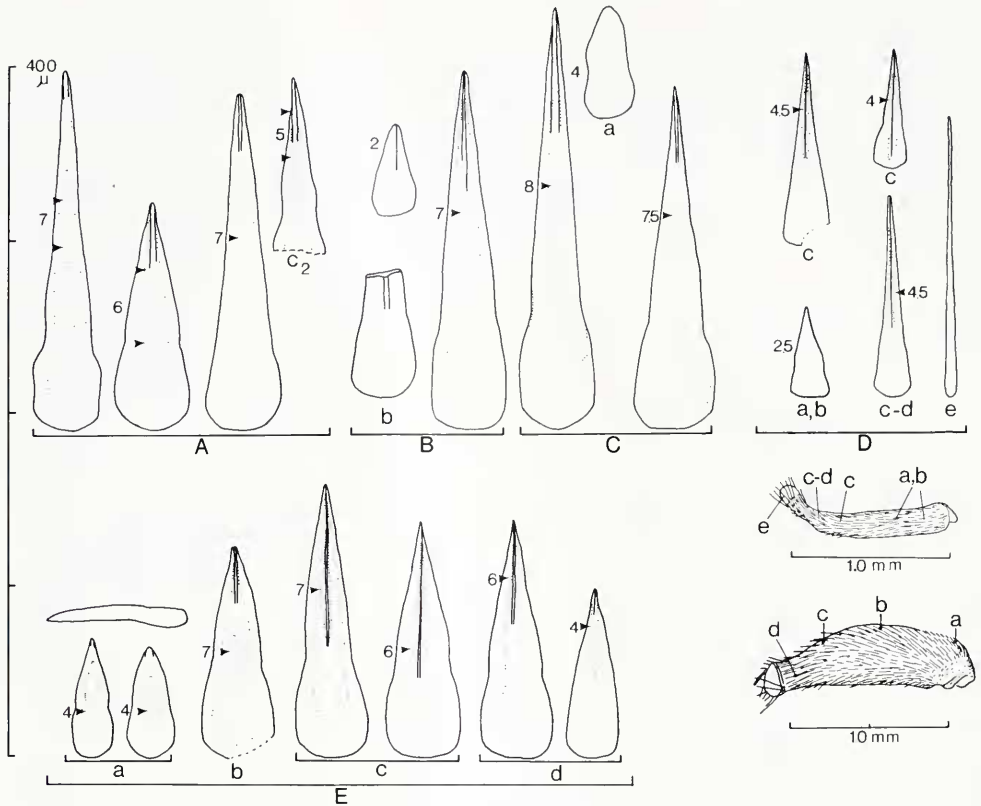


FIGURE 7. Variation in spicule morphology of *Prochaetoderma yongei* n. sp. from the North American Basin. A–C. spicules from junction of trunk and posterior, unless indicated otherwise; A. from single specimen from 805 m (CH-88 Sta. 207); B. from 3 specimens from 1470 m (type locality); C. from single specimen from 530 m (CH-58 Sta. 105); D. spicules from paratype no. 4, figured just below, immature specimen (type locality); E. spicules from paratype no. 3 figured at lower right, a short, stubby specimen from 805 m (CH-88 Sta. 207).

blade are straight in *P. raduliferum* and convex in *P. yongei*; the base in *P. raduliferum* is round, and in *P. yongei* it is flared proximally.

**Radula and jaws.** The jaws and teeth are typical for the family and small (Fig. 14  $\mu\text{m}^3$ ). Tooth length ranges up to 90  $\mu\text{m}$ ; jaw length and width range up to 365 and 128  $\mu\text{m}$ , respectively. The entire radula has 8 to 11 rows of teeth. The central radula plate is short, up to 26  $\mu\text{m}$ , and broad, up to 8  $\mu\text{m}$ ; the ends are directed posteriorly.

#### Morphological variation

Several populations of *Prochaetoderma yongei*, identified by similarity of spicule and radula morphology, were examined to determine the variability that occurs within this species and could therefore be expected in other species of the family Prochaetodermatidae.

**Spicules.** Several spicules from the dorsal junction of trunk and posterior were drawn and compared for 24 specimens from four stations along the Gay Head-Bermuda transect in the North American Basin and from five stations between the northern



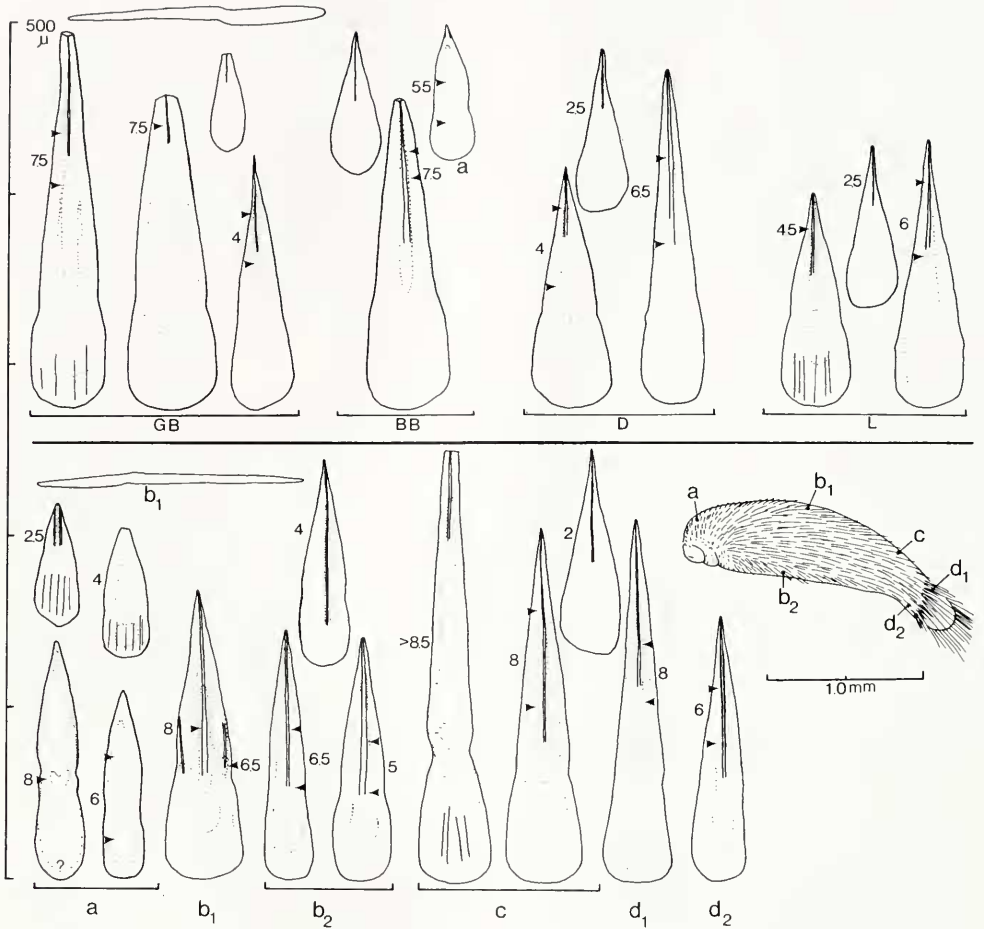


FIGURE 8. Variation in spicule morphology of *Prochaetoderma yongei* n. sp. from the eastern Atlantic. Upper row: spicules from junction of trunk and posterium, unless otherwise indicated. GB, off Great Britain (West European Basin), 2091 m (INCAL DS-01); BB, Bay of Biscay (West European Basin), 1922 m (SARSIA 65); D, Cape Verde Basin, 1624 m (AII-31 Sta. 142); L, Angola Basin, 1427 m (AII-42 Sta. 202). Lower row: spicules from paratype no. 2, 1546 m, Namibia Basin. Upper and middle left, lateral views showing offset blade.

West European Basin and Namibia Basin in the eastern Atlantic; spicules were measured from fifteen of these specimens (Table III) and scanning electron photomicrographs were made of spicules from three (Fig. 7A-C). Variation in shape is as great among spicules from a single specimen (Fig. 7A) as among spicules from far-distant populations (e.g., Namibia Basin at 1546 m, Fig. 8, lower row, and North American Basin at 530 m, Fig. 7C). Greatest blade length decreases with depth in the western Atlantic and from north to south in the eastern Atlantic between the West European Basin and Angola Basin; in the Namibia Basin, blade length again increases (Table III, Fig. 8).

Spicule length is not correlated with body length, except that very small juveniles have relatively small spicules (Fig. 7D). In a test of significance, the longest spicule

TABLE III

Range in spicule dimensions from body region c, in *Prochaetoderma yongei* and *Spathoderma clenchi* ( $\mu\text{m}$ ) (number of specimens in parentheses)

	Total length	Blade length	Base length	Blade width	Base width
<i>P. yongei</i>					
<i>No. American Basin</i>					
AII-12 Sta. 73 (6) (1400 m)	101-207	60-148	38-70	20-34	27-47
CH-88 Sta. 207 (3) (800 m)	128-202	81-158	40-61	22-32	34-45
CH-58 Sta. 105 (1) (500 m)	202-241	148-178	54-63	27-32	40-50
<i>West European Basin</i>					
INCAL DS-01 (1)	151-225	99-164	45-63	22-43	34-52
SARSIA 65 (1)	184-220	112-153	68-72	32-36	47-50
<i>Cape Verde Basin</i>					
AII-31 Sta. 142 (1)	144-198	88-142	56	25-29	38-47
<i>Angola Basin</i>					
AII-42 Sta. 202 (1)	126-162	74-108	50-52	29-32	40-43
<i>Namibia Basin</i>					
AII-42 Sta. 191 (1)	178-252	122-173	50-79	29-34	40-45
<i>S. clenchi</i>					
<i>No. American Basin</i>					
AII-30 Sta. 131 (1) (2178 m)	101-202	43-119	68-90	22	27-43
AII-12 Sta. 73 (4) (1400 m)	128-232	56-155	72-90	16-25	34-50
<i>West European Basin</i>					
INCAL DS-01 (1)	122-232	54-146	68-86	11-22	32-45
<i>Namibia Basin</i>					
AII-42 Sta. 194 (1)	142-227	74-130	56-97	22	25-43

from a specimen was not correlated with specimen length in nine North American Basin specimens from 1470 m (AII-12 Sta. 73,  $r = .25$ ) and in 6 specimens from 805 m (CH-88 Sta. 207,  $r = .36$ ). In the specimens from the 805 m station mean body length was 1.6 mm and greatest length of spicules was 202  $\mu\text{m}$ , whereas the mean body length of the specimens from 1470 m was significantly greater, 2.1 mm ( $P < .02$ ), but greatest spicule length was about the same, 207  $\mu\text{m}$ . On the other hand, in the eastern Atlantic, body length of a specimen from 2091 m off Scotland (INCAL



DS-01) was 1.6 mm and greatest spicule length 225  $\mu\text{m}$ , whereas a specimen of the same body length from 1427 m in the Angola Basin (AII-42 Sta. 202) had spicules with greatest length of only 162  $\mu\text{m}$  (Fig. 8GB and L).

It is concluded that spicule shape and ornamentation, but not size, are of taxonomic significance in defining a widely distributed species of Prochaetodermatidae.

*Radula.* Jaws and radulae of 20 specimens ranging in length from 1.1 to 2.5 mm were examined, 19 from the North American Basin and 1 from the Namibia Basin. Of the former, 6 were from short, stubby specimens at 805 m and 13 from long, slender specimens at 1470 m (*cf.*, specimens in Figs. 6 and 7). For the North American Basin, greatest jaw length at 805 and 1470 m depths was 365 and 360  $\mu\text{m}$ , respectively; greatest tooth length, 90 and 85  $\mu\text{m}$ ; and greatest length of the central plate, 25 and 26  $\mu\text{m}$ . In the specimen from the Namibia Basin, jaw length was 336  $\mu\text{m}$ , tooth length 83  $\mu\text{m}$ , and length of central plate 25  $\mu\text{m}$ . Morphology of the central plate was similar in all three locations (Fig. 14,  $y^1-y^3$ ).

The differences in size among radulae and jaws and in morphology of the central plate seem too slight in the three locations to indicate species differences.

*Body shape.* Body shape is difficult to quantify in the highly contractible and extensible species of Prochaetodermatidae. The only measurements that are correlated to each other in all populations measured are posterium length to trunk length ( $P < .02$  to  $<.001$ ); other measurements such as trunk diameter to trunk length are not correlated at all, or are correlated in only some populations. Yet specimens with similar spicule morphology from different populations may appear to have a distinctive body shape, *e.g.*, short and stubby from 805 m in the North American Basin or long and slender 600 meters further downslope (Figs. 6, 7). Differences between mean values for the characters measured are statistically significant for some characters between some populations, but there is no consistent or clinal pattern (Table IV).

Therefore, to compare body shapes, an overall coefficient of similarity was determined for each of seven populations of *Prochaetoderma yongei*, identified as such by spicule morphology, and for comparison, for one population of *Spathoderma clenchi*, n. sp. (*q.v.*) which is very similar in shape but not in spicule morphology. The mean character difference (M.C.D.) was computed from five characters: trunk length, trunk diameter, posterium length, posterium diameter, and ratio of posterium length to trunk length (Table IV). Every population of *P. yongei* was compared with every other *P. yongei* population, a total of 21 comparisons; the *S. clenchi* population was compared with each of the 7 *P. yongei* populations. For each comparison between two populations, the absolute values of the differences between the five pairs of mean character values were summed and averaged, each mean character value having first been reduced by setting the maximum value for that character at 100.

The equation used for mean character difference by Sneath and Sokal (1973) is

$$\frac{1}{n} \sum_{i=1}^n |X_{ij} - X_{ik}|$$

where  $n$  = number of characters and  $X_{ij}$ ,  $X_{ik}$  = mean values of populations  $j$ ,  $k$  for character  $i$ . The lower the mean character difference is between two populations, the more similar they are.

The resulting six mean character differences (M.C.D.) for each population of *P. yongei* were summed to give an overall value (Table V, Total M.C.D.). A comparison of these summed M.C.D.'s indicates that the total for any one population is not strikingly different from that of any other, although the range in values are rather large. The highest value for summed M.C.D.'s (67.7) occurs at one end of the depth range,

TABLE IV

Mean value, standard deviation, and sample number for five characters in seven populations of *Prochaetoderma yongei* and one population of *Spathoderma clenchi*

Station and depth	Trunk length mm		Posterior length mm		Trunk diameter mm		Posterior diameter mm		Posterior length: Trunk length	
	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.
	(n)		(n)		(n)		(n)		(n)	
<i>Prochaetoderma yongei</i>										
<i>No. American B.</i>										
CH-88 Sta. 207 805-811 m	1.11	.23	.36	.08	.37	.05	.22	.03	.33	.09
	(70)		(70)		(70)		(70)		(70)	
CH-50 Sta. 87 1102 m	1.38	.24	.48	.12	.34	.07	.19	.02	.35	.06
	(35)		(35)		(36)		(36)		(35)	
All-30 Sta. 128 1254 m	1.39	.23	.43	.08	.33	.05	.21	.03	.31	.04
	(44)		(44)		(42)		(44)		(44)	
All-12 Sta. 73 1470-1330 m	1.55	.27	.54	.11	.35	.06	.19	.03	.35	.06
	(137)		(137)		(136)		(133)		(137)	
CH-88 Sta. 209 1501-1693 m	1.16	.30	.38	.09	.31	.07	.21	.03	.34	.05
	(46)		(46)		(44)		(46)		(46)	
All-30 Sta. 131 2178 m	1.61	.25	.53	.17	.33	.07	.21	.04	.33	.08
	(15)		(15)		(15)		(15)		(15)	
<i>Namibia B.</i>										
All-42 Sta. 191 1600 m	1.39	.19	.41	.09	.38	.05	.22	.03	.30	.05
	(43)		(43)		(43)		(43)		(43)	
<i>Spathoderma clenchi</i>										
<i>No. American B.</i>										
All-30 Sta. 131 2178 m	1.01	.22	.51	.14	.35	.05	.22	.03	.51	.12
	(35)		(35)		(37)		(32)		(35)	

that is, in the population from the shallowest station; the lowest value (45.0) occurs in one of the populations at mid-depth range. The values for both total and range in M.C.D.'s in the population geographically most distant from the others (Namibia Basin) fall well within the values for other populations.

High total M.C.D. values, such as 67.7 for the short, stubby forms at the shallow station (Sta. 207) and 65.0 for the long, slender forms at the type locality at mid-depth range (Sta. 73), do not contain any taxonomic information on how these populations differ (Cain and Harrison, 1958); however, an examination of actual measurements (Table IV) indicates that in these two populations, differences in length are responsible for the high total M.C.D. values.

Body shape in specimens of *P. yongei* and *Spathoderma clenchi* is often so similar that species determination was always based on spicule morphology. However, the average M.C.D. value of the seven comparisons between the single *S. clenchi* population

TABLE V

Total, range and average mean character differences (M.C.D.'s) between seven populations of *Prochaetoderma yongei*, and range and average M.C.D.'s between one population of *Spathoderma clenchi* and the seven *P. yongei* populations

Station	Depth m	Total M.C.D.*	Range of M.C.D.'s	Average M.C.D.
<i>Prochaetoderma yongei</i>				
<i>No. American B.</i>				
CH-88 Sta. 207	805-811	67.7	5.8-16.7	11.3
CH-50 Sta. 87	1102	51.2	4.9-12.9	8.5
AII-30 Sta. 128	1254	45.0	4.7-10.5	7.5
AII-12 Sta. 73	1470-1330	65.0	4.8-16.7	10.8
CH-88 Sta. 209	1501-1693	60.7	5.8-15.1	10.1
AII-30 Sta. 131	2178	59.8	4.8-15.5	10.0
<i>Namibia B.</i>				
AII-42 Sta. 191	1600	56.3	4.7-13.1	9.4
<i>Spathoderma clenchi</i>				
<i>No. American B.</i>				
AII-30 Sta. 131	2178	**	14.9-19.7	17.2

\* See text for explanation.

\*\* Total M.C.D.'s between *S. clenchi* and *P. yongei* are meaningless.

and the seven *P. yongei* populations is 17.2, much higher than the average values—7.5 to 11.3—among *P. yongei* populations, although there is considerable overlap in the ranges of values in the two species. Thus mean character difference seems to be a sensitive measure of similarity in body shape within a species and of dissimilarity between two species.

The only character that is significantly different in all comparisons between the two species is the ratio of postterium length to trunk length (*t*-test of the means,  $P < .001$  for all populations), and it is this character difference which accounts for the high M.C.D. values in *S. clenchi*. In contrast, the shallowest population of *P. yongei* was not significantly different from any other population of *P. yongei* in mean postterium- to trunk-length ratio, although it is the population with the highest value for total M.C.D. and the appearance of being most different in body shape. On the other hand, this ratio is not a perfect species indicator, for among all 7 *P. yongei* populations it was significantly different in 5 out of the total 21 comparisons.

It is concluded that (1) there is not sufficient difference in body shape, as quantified by mean character difference, among populations of *P. yongei* to consider that any of them belong to a different species; and (2) the ratio of postterium length to trunk length is an important taxonomic character in species of Prochaetodermatidae.

### Distribution

*Prochaetoderma yongei* is very widely distributed on the continental slope between 800 and 2000 m in the northwestern and eastern Atlantic (Table I; Fig. 1, solid circles). It does not occur in samples taken between Cape Hatteras and the Argentine Basin

in the western Atlantic or from depths less than 450 or greater than 2200 m. The samples in which it was taken in the eastern Atlantic are distributed at very great but rather even distances between 58°N and 23°S.

In the North American Basin, *P. yongei* is very abundant in both quantitative and nonquantitative samples; in the eastern Atlantic it is up to a hundredfold less abundant in sled trawls and was not taken in quantitative samples (Tables I, VII). Between depths of 1300 and 2100 m in both the northwestern and northeastern Atlantic *P. yongei* occurs sympatrically with the confamilial species *Spathoderma clenchi* (q.v.). In samples containing both species, *P. yongei* is the more abundant at depths less than 1800 m in the western Atlantic and 1900 m in the eastern Atlantic. (Anchor dredge samples are disregarded because of their inherent sampling bias.)

A single specimen of *P. yongei* taken from 530 m off Gay Head is 2.8 mm long, large for the species. A single specimen from 5042 m (CH-50 Sta. 81) is probably mislabeled.

#### *Specimens examined*

A total of 3122 specimens was examined, 2987 from the western Atlantic and 135 from the eastern Atlantic (Table I).

#### Genus *Spathoderma* n.g.

With characters of the family. Spicules spatulate, with flat base and relatively long, narrow blade rounded in cross-section, bent outward from body.

Distribution (based in part on species to be described): Atlantic continental slopes and abyssal plains.

From *spatha* (L.), a spatula.

Type species: *Spathoderma clenchi* n. sp., North American Basin.

#### *Spathoderma clenchi* n. sp.

Figs. 1, 3D–G, 4D, F, 9, 14 c<sup>1</sup>, c<sup>2</sup>; Tables I, III, IV, V, VII

*Prochaetoderma* sp. c. Scheltema, 1981, *Malacologia* **20**: 363.

*Prochaetoderma* sp. A. Rowe, Polloni, and Haedrich, 1982, *Deep Sea Res.* **29**: Table 2.

*Prochaetoderma* sp. A. Scheltema, 1985, in L. Laubier and C. Monniot, eds., *Peuplements Profonds du Golfe de Gascogne: Campagnes BIOGAS*, IFREMER, Brest, pp. 391–396, Tables 1, 2, 3.

*Diagnosis*: Opaque, less than 2½ mm long, posterium ⅓ total length; oral-shield spicules indistinct; spicules bent slightly outwards and oriented parallel to long axis of body, without ornamentation, greatest length 232 µm, blades narrow with concave sides, bent sharply outwards, base with parallel sides; greatest jaw length 435 µm; greatest tooth length 100 µm; central radula plate long and relatively narrow, greatest length 45 µm.

This species is named in honor of Dr. William J. Clench, who first encouraged me to study mollusks.

Holotype: North American Basin, 39°38.5'N, 70°36.5'W, 2178 m (ATLANTIS II-30 Sta. 131, 18/XII/66). USNM No. 850209.

Illustrated paratypes:

Nos. 1, 2: Type locality. USNM Nos. 850210 (No. 1), 850211 (No. 2).



No. 3: West European Basin, 57°59.7'N, 10°39.8'W, 2091 m (INCAL DS-01, 15/VII/76). MNHN, Paris.

No. 4: West European Basin, 55°07.7'N, 12°52.6'W, 2897 m (INCAL DS-09, 20/VII/76). MNHN, Paris.

### Description

*External morphology.* *Spathoderma clenchi* is a small, opaque species with bent spicules which extend out from the body most noticeably at the junction of trunk and posterium; they are oriented parallel to the long axis of the body except ventrally, where they diverge along the midline (Fig. 3D–F). Average total body length at the type locality is 1.5 mm; greatest length is 2.2 mm. Both average and greatest trunk diameter are 0.4 mm. Posterium length is about  $\frac{1}{3}$  total length. Mean posterium length is 0.5 mm, and greatest length 0.9 mm; posterium diameter averages 0.2 mm and greatest diameter is 0.3 mm. The mean index of posterium to trunk length is 0.51, ranging from 0.27 to 0.87. The margin of the cloaca in lateral view is oblique. The oral shield is slightly larger than in *Prochaetoderma yongei* (Fig. 3G); oral shield spicules are present but not obvious.

Holotype: Total length 2.1 mm, trunk 1.4 mm by 0.4 mm, posterium 0.7 mm by 0.2 mm, index of posterium to trunk 0.50. Oral shield 0.06 by 0.12 mm; index of oral shield to trunk diameter 1.80.

*Spicules.* The spicules of *S. clenchi* lack ornamentation except for faint ridges on the blade seen only by scanning electron microscopy and an occasional subdued keel (Figs. 4D, F; 9). The sides of the base are straight and usually parallel; proximally the base is rounded or broadly triangular. In some spicules the base widens into a bulge at the waist. The sides of the blade are concave proximally at the waist where the blade rapidly narrows, except in spicules from region  $a_1$  and ventral region  $b_2$  where the blade may have convex sides.

The blade is narrow and sharply or roundly pointed. The isochromes are symmetrical. The thickest part of the spicule is at or just proximal to the waist in spicules from region  $b_1$ ; further posteriorly along the body, the thickest part is the blade. The width of the base is usually narrower in spicules from the posterium (region  $d$ ) than in those from the trunk. In lateral view the blade is bent sharply outwards, except in region  $a$  and in ventral region  $b_2$  where the blade is bent towards the body. Spicules from the ventral side of the body are smaller than those from the dorsal side. A few short, thin spicules with a short distal point are scattered on the body.

Ranges in dimensions of spicules from region  $c$  are given for four populations in three basins in Table III.

*Radula.* The jaws and teeth, examined in nine specimens, are large and typical for the family (Fig. 14  $c^1$ ,  $c^2$ ). Tooth length ranges up to 100  $\mu\text{m}$ , and jaw length and width up to 435 and 151  $\mu\text{m}$ , respectively. The radula has 8 to 10 rows of teeth. The central radula plate is curved and long, up to 45  $\mu\text{m}$ , and slender, up to 6  $\mu\text{m}$  wide, with the ends rounded or somewhat pointed.

### Distribution

*Spathoderma clenchi* has the same geographic range as *Prochaetoderma yongei*: from the northwestern to the northeastern Atlantic and south to the Namibia Basin in the eastern Atlantic; like *P. yongei* it is not found south of Cape Hatteras in the western Atlantic (Fig. 1, triangles). In vertical range, the two species overlap on the continental slope, but *S. clenchi* ranges deeper onto the abyssal rise, down to 3356 m

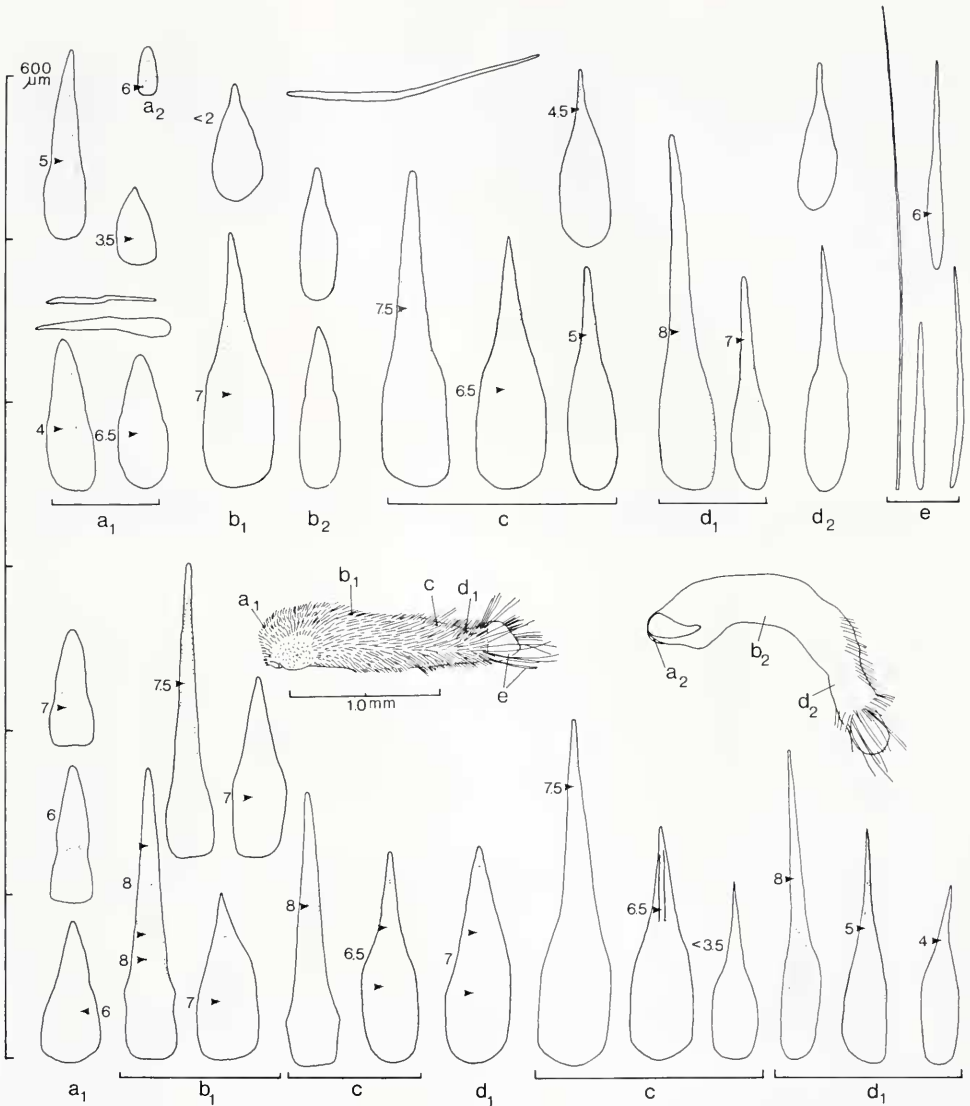


FIGURE 9. Spicules of *Spathoderma clenchi* n.g. n. sp. *Upper row*:  $a_1$ - $e$  from paratypes no. 1, left specimen, and no. 2, right specimen, 2178 m, North American Basin (type locality). *Lower row*:  $a_1$ - $d_1$  at left, spicules from several specimens from 1470 m, North American Basin (A II-12 Sta. 73);  $c$  and  $d_1$  at right, spicules from paratype no. 3, 2091 m, West European Basin (region  $d_1$  spicules somewhat oblique). Uppermost center spicule, lateral view showing blade (to right) bent outwards away from body; lateral views of  $a_1$  spicules, to left, are bent somewhat towards body.

(Table I). It is commonly found in samples taken at depths over 2000 m, and is sometimes abundant (Table VII).

#### *Specimens examined*

A total of 1480 specimens was examined, 682 specimens from the western Atlantic and 798 from the eastern Atlantic (Table I).



Genus *Chevroderma* n. g.

With characters of the family. Spicules asymmetrical, base of spicules long, with a longitudinal groove and regularly spaced, chevron-shaped cross grooves reflecting crossed fibers of cuticle (Fig. 5F). Spicules of trunk flat-lying and arranged obliquely, diverging on each side of ventral midline, spiralling up dorsally and posteriorly, and meeting at a slight or pronounced angle along dorsal midline (Fig. 3). Thickest part of spicule is dorsal to longitudinal groove, overlapping ventral, thin side of next adjacent spicule dorsal to it (Fig. 10, upper left).

Distribution: Lower continental slopes and abyssal plains of the Atlantic and Pacific; Aleutian Trench.

From *chevron* (Fr.), a chevron.

Type species: *Chevroderma turnerae* n. sp.

*Chevroderma turnerae* n. sp.

Figs. 1, 3 L-P, 5 B, D, F, 10, 15 t<sup>1</sup>-t<sup>3</sup>; Tables I, VI, VII

*Prochaetoderma* sp. C. Scheltema, 1985, in L. Laubier and C. Monniot eds., *Peuplements Profonds du Golfe de Gascogne: Campagnes BIOGAS, IFREMER*, Brest, pp. 391-396, Tables 1, 2, 3.

*Diagnosis*: Large, opaque, up to 5½ mm in length and 0.8 mm in diameter, with a long posterium  $\frac{2}{5}$  or more total length; large oral shield and prominent oral shield spicules; spicules converge at pronounced angle along dorsal midline; trunk spicules up to 300 µm with long base and wide, short blade bluntly pointed, thickened proximal to waist; radula and jaws large, teeth up to 140 µm long, jaws up to 700 µm long, and central plate long, up to 50 µm, narrow, and curved.

This species is named in honor of Prof. Ruth D. Turner, who has given me many years of encouragement and advice.

Holotype: North American Basin, 35°50.0'N, 64°57.5'W, 4833 m (ATLANTIS II-24 Sta. 122, 21/VIII/66). USNM No. 850213.

## Illustrated paratypes:

Nos. 1, 3: Type locality. USNM Nos. 850214 (No. 1), 850216 (No. 3).

No. 2: Angola Basin, 14°49'S, 9°56'E, 3797 m (ATLANTIS II-42 Sta. 195, 19/V/68). USNM No. 850217.

No. 4: Brazil Basin, 00°46.0'S, 29°28.0'W, 3459 m (ATLANTIS II-31 Sta. 156, 14/II/67). USNM No. 850219.

No. 5: West European Basin, 47°32'N, 9°35.9'W, 4237 m (BIOGAS-VI CP-14, 23/X/74). MNHN, Paris.

No. 6: Canary Basin, 27°14.9'N, 15°36.3'W, 2988 m (DISCOVERY 6711, 19/III/68). USNM No. 850221.

No. 7: Argentine Basin, 37°13.3'S, 52°45.0'W, 3305 m (ATLANTIS II-60 Sta. 259, 26/III/71). USNM No. 850223.

*Description*

*External morphology*. *Chevroderma turnerae* is large for a prochaetodermatid species with total body length averaging from 2.8 to 3.8 mm in three widely separated populations and ranging up to 5½ mm (Fig. 3L). Trunk diameter averages 0.5 mm, with greatest diameter 0.8 mm (Table VI). The posterium is long, from  $\frac{2}{5}$  to nearly

TABLE VI

Mean value, standard deviation, and sample number for five characters in four species of *Chevroderma* (*C. turnerae*, *C. gauson*, *C. scalpellum*, and *C. whitlatchi*)

Station and depth	Trunk length mm		Posterior length mm		Trunk diameter mm		Posterior diameter mm		Posterior length: Trunk length	
	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.
	(n)		(n)		(n)		(n)		(n)	
<i>Chevroderma turnerae</i>										
<i>No. Amer. B.</i>										
All-24 Sta. 122 4833 m	1.9 (11)	.84	1.6 (10)	.68	0.5 (11)	.13	0.3 (11)	.09	.71 (10)	.20
<i>W. European B.</i>										
NOR. 113-EO13 4760 m	2.0 (43)	.72	1.6 (43)	.72	0.5 (45)	.13	0.3 (45)	.05	.80 (43)	.23
<i>Argentine B.</i>										
All-60 Sta. 245 (subsample) 2707 m	1.7 (16)	.50	1.1 (16)	.40	0.5 (16)	.12	0.3 (16)	.09	.69 (16)	.21
<i>C. gauson</i>										
<i>W. European B.</i>										
CH-106 Sta. 330 4632 m	1.7 (8)	.52	0.8 (8)	.21	0.6 (8)	.14	0.3 (8)	.07	.52 (8)	.12
<i>C. scalpellum</i>										
<i>Angola B.</i>										
All-42 Sta. 202 1427 m	1.0 (50)	.27	0.5 (50)	.15	0.4 (50)	.08	0.3 (50)	.05	.52 (50)	.12
<i>C. whitlatchi</i>										
<i>Aleutian Trench</i>										
SEVENTOW H-39 7298 m	1.0 (31)	.43	0.6 (31)	.36	0.3 (31)	.02	0.2 (31)	.06	.63 (31)	.14
<i>Panama B.</i>										
ALVIN dives 3912 m	0.9 (31)	.35	0.6 (31)	.19	0.3 (31)	.08	0.2 (31)	.05	.71 (31)	.26

½ body length; it averages 1.1 to 1.6 mm in length in three populations, with greatest length 2.9 mm, and 0.3 mm in diameter, with greatest diameter 0.5 mm. The posterior to trunk ratio averages 0.69 to 0.80, but the range is very large, from 0.32 to 1.36. The spicules of the trunk meet at a distinct angle along the dorsal midline (Fig. 3N).

The long spicule blades of the posterium extend out from the body. There are two rows of prominent oral shield spicules; the oral shield is distinctively large (Fig. 3O, P). The margin of the cloaca in lateral view is slanted.

Holotype: Total length 4.7 mm, trunk 2.8 by 0.7 mm; posterium 1.9 by 0.4 mm; index of posterium to trunk 0.68. Oral shield 0.14 by 0.17 mm; index of oral shield to trunk diameter 3.40.

*Spicules.* Trunk spicules are thick, with a long base relative to a short, wide blade that tapers to a rounded point (Figs. 5B, D, and 10, *b*, *c*). Greatest length is about 300  $\mu\text{m}$ . The base is slightly rotated about its long axis. Greatest thickness, up to 8.5  $\mu\text{m}$ , is about midway lengthwise, proximal to the waist. The sides of the base are somewhat convex, with the dorsal edge curved more than the ventral edge; the proximal end is rounded to somewhat pointed. The waist is either distinct or indistinct. The longitudinal groove usually runs the entire length of the base and often onto the blade. The blade is straight, or bent slightly outward. Spicules from the ventral side of the trunk are shorter but not narrower than spicules from the lateral and dorsal sides; the waist is not distinct (Fig. 10 *b*<sub>2</sub>, *c*<sub>2</sub>).

Oral shield spicules are large and thick (Fig. 10*a*<sub>2</sub>); spicules at the junction of anterium and trunk (*a*<sub>1</sub>) are thick and symmetrical. Spicules of the posterium (*d*) are more nearly symmetrical than those of the trunk; some are quite narrow and thickest at the waist, similar to spicules of *C. gauson* n. sp. (*q.v.*). Trunk spicules of immature specimens are sharply pointed (Fig. 10B left).

Faint ridges occur on some or all of the trunk spicules in populations other than those from the North American Basin, which lack ridges. At least some spicules from the posterium are ridged in every population (ridges not illustrated).

*Radula:* The teeth and jaws from ten specimens were examined; they are large and typical for the family (Fig. 15 *t*<sup>1</sup>–*t*<sup>3</sup>). Teeth range up to 140  $\mu\text{m}$  in length; jaws range up to 700  $\mu\text{m}$  in length and 300  $\mu\text{m}$  in width, but are usually between 500 and 600  $\mu\text{m}$  in length and between 200 and 250  $\mu\text{m}$  in width. The central plate is long, up to 50  $\mu\text{m}$ , relatively narrow, up to 10  $\mu\text{m}$ , curved, and tapered at the ends. The brush membrane and the wing may be thickened, or tanned, in distal teeth.

### *Morphological variation*

Greatest geographic variations in spicule morphology are in base width and degree of asymmetry. Spicules from specimens from the North American and deepest West European Basin have narrow bases relative to most other populations (Fig. 10, upper row and W spicules 1, 5). Wide-based spicules occur along with narrow-based spicules in the populations of the Brazil and Argentine Basins and the West European Basin (Fig. 10B, A, W spicules 3, 4). Spicules are all relatively wide-based from specimens taken from the Canary Basin southwards in the eastern Atlantic (Fig. 10C, An, N).

Most samples of *Chevroderma turnerae* are either too small for statistical analysis of body shape (see Table I) or comprised of mostly immature specimens. Samples from three widely separated geographic regions—North American Basin (ATLANTIS II-24 Sta. 122), West European Basin (NORATLANTE 113-E013), and Argentine Basin (ATLANTIS II-60 Sta. 245)—show no significant difference between means of five body measurements among the three populations except in posterium length (Table VI). In the Argentine Basin population, posterium length is statistically—and noticeably—shorter than in the other two populations. However, the ratio of posterium length to trunk length is not significantly different among the three populations.

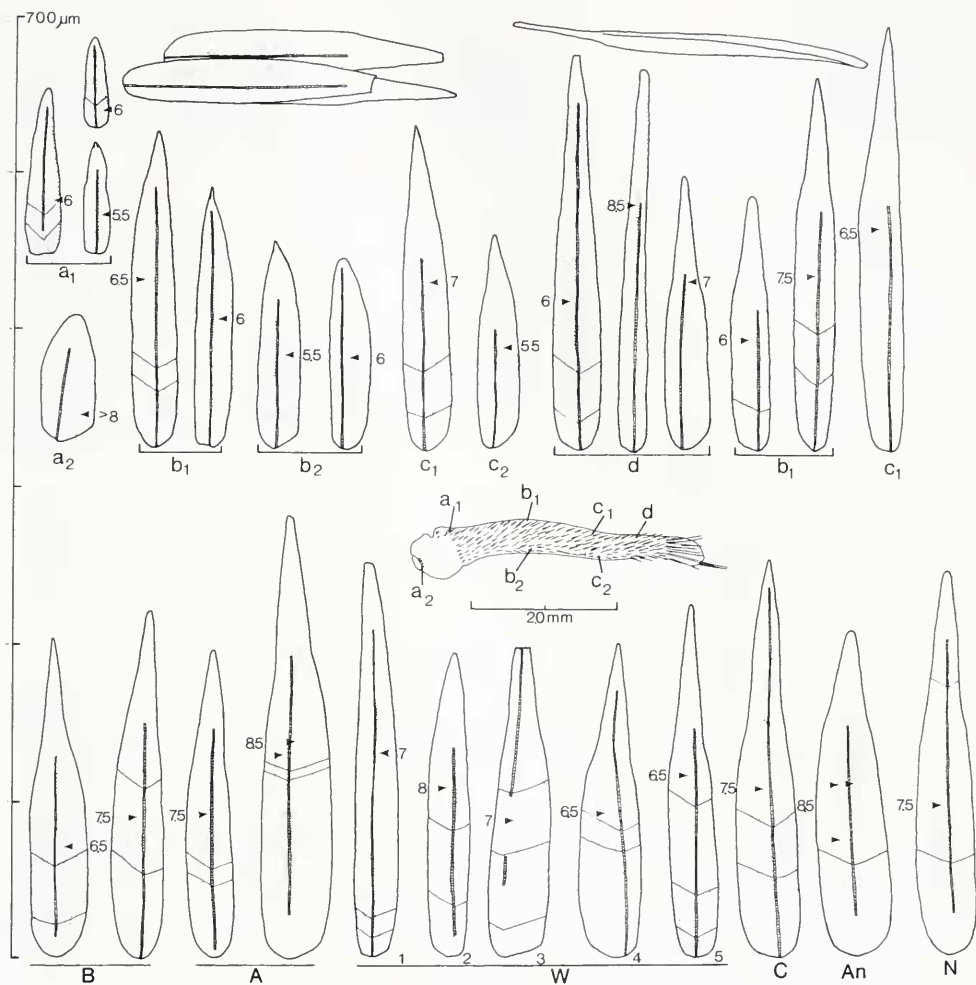


FIGURE 10. Spicules of *Chevroderma turnerae* n.g. n. sp. Upper row:  $a_1$ – $d$  at left, paratype no. 1 (figured specimen), and  $b_1$ ,  $c_1$  at right, paratype no. 3, 4833 m, North American Basin (type locality); upper left, overlapped spicules showing *in situ* arrangement, anterior end to left, dorsal side uppermost; upper right, lateral view showing rotation and outward bend of short blade. Lower row: variation in morphology of spicules from trunk regions  $b_1$  and  $c_1$ : B, immature specimen, paratype no. 4, 3459 m, Brazil Basin; A, two specimens from 3305 m, Argentine Basin, right spicule paratype no. 7; W, several specimens from West European Basin: spicule 1 from a deep station at 4823 m (INCAL CP-10), spicules 2 and 3 from shallower stations at 2897 and 2634 m (INCAL DS-09 and OS-01), spicules 4 and 5 from 4237 and 4706 m at stations further east in the Bay of Biscay (paratype no. 5 and BIOGAS VI CP-17); C, paratype no. 6, 2988 m, Canary Basin; An, paratype no. 2, 3797 m, Angola Basin; N, immature specimen, 4184 m, Namibia Basin (WALDA DS-04).

The larger size, but not the shape, of spicules also differentiates the shallower Argentine Basin population of *C. turnerae* from the other two populations (Fig. 10A).

Jaw length in one of two Argentine Basin specimens is great (700  $\mu$ m) compared to jaw length in five specimens from three other widely separated populations (493–580  $\mu$ m, North American, West European, and Angola Basins). However, jaw length

in the second Argentine Basin specimen (560  $\mu\text{m}$ ) falls within the limits measured in the other three populations.

On the bases of body measurements and spicule and radula morphology, the Argentine Basin continental slope populations of *C. turnerae* are considered to be small, short-tailed members of the species.

### *Distribution*

*Chevroderma turnerae* is a cosmopolitan abyssal species of the Atlantic basins, absent only in samples from the Guyana and Iberian Basins (Table I; Fig. 1, open circles). Its depth range is also great, from a little over 2100 m to 5208 m. It is most commonly found at depths greater than 3000 m except in the Argentine Basin, where it was taken in largest numbers at depths less than 3000 m.

*Chevroderma turnerae* has never been taken in large numbers at any one locality, even with an epibenthic sled trawl; the greatest densities sampled quantitatively were in the Bay of Biscay (Tables I, VII).

### *Material examined*

Five hundred thirty-eight specimens were examined, 222 from the western Atlantic and 316 from the eastern Atlantic.

#### *Chevroderma gauson* n. sp.

Figs. 1, 3Q–T, 5A, 11, 15 g<sup>1</sup>, g<sup>2</sup>; Tables I, VI

*Prochaetoderma* sp. D. Scheltema, 1985, in L. Laubier and C. Monniot, eds., *Peuplements Profonds du Golfe de Gascogne: Campagnes BIOGAS*, IFREMER, Brest, pp. 391–396, Tables 1, 2.

*Diagnosis*: Opaque, broad, with very long spicules distinctly bent outward from body; greatest body length 3.6 mm, greatest diameter 0.8 mm, posterium  $\frac{1}{3}$  total length and broad; oral shield spicules small, indistinct; trunk spicules up to nearly 500  $\mu\text{m}$ , thickest at distinct waist, blade long, narrow, and bent outwards, longitudinal groove distinct to faint; radula large, teeth up to about 130  $\mu\text{m}$  in length, jaws up to 626  $\mu\text{m}$ , central plate long, up to 48  $\mu\text{m}$ , wide and thick with a shallow groove, ends blunt.

The species name means "bent outwards."

Holotype: West European Basin, 50°43.5'N, 17°51.7'W, 4632 m (CHAIN-106 Sta. 330, 24/VIII/72). USNM No. 850226.

### Illustrated paratypes:

No. 1: West European Basin, 50°04.7'N, 15°44.8'W, 4426 m (CHAIN-106 Sta. 328, 23/VIII/72). USNM No. 850229.

No. 2: Type locality. USNM. No. 850227.

No. 4: West European Basin, 48°19.2'N, 15°15.9'W, 4829 m (INCAL 0S-02, 2/VIII/76). MNHN, Paris.

No. 5: West European Basin, 48°19.2'N, 15°23.3'W, 4829 m (INCAL WS-03, 1/VIII/76). MNHN, Paris.

### *Description*

*External morphology*. *Chevroderma gauson* is a moderately large, broad, opaque species with very long spicules which are bent outward and spiral upwards and pos-



TABLE VII

Vertical distribution, average sample number, and greatest density of three Prochaetodermatidae species in the North American and West European Basins

Depth m	Samples (N)*		No. Amer. B.				W. Europ. B.			
	No. Amer. B.	W. Europ. B.	Samples with species	No. individ. ( $\Sigma\bar{X}$ )	$\Sigma X/N = \bar{X}$	$\frac{s^2}{\bar{X}}$	Samples with species	No. individ. ( $\Sigma\bar{X}$ )	$\Sigma X/N = \bar{X}$	$\frac{s^2}{\bar{X}}$
<i>Prochaetoderma yongei</i>										
0-500	6	3	1	3	0.5	3.0	0	—	—	—
501-1000	2	6	2	167	83.5	163.0	0	—	—	—
1001-1500	3	4	3	1942	647.3	422.5	1	19	4.8	18.8
1501-2000	1	14	1	435	435.0	—	5	17	1.2	5.3
2001-2500	5	45	4	281	56.2	95.2	3	8	0.2	3.2
2501-3000	6	23	0	—	—	—	0	—	—	—
3001-3500	1	6	0	—	—	—	0	—	—	—
3501-4000	7	5	0	—	—	—	0	—	—	—
4001-4500	1	43	0	—	—	—	0	—	—	—
4501-5000	22	28	0	—	—	—	0	—	—	—
>5000	4	0	0	—	—	—	—	—	—	—
Greatest density sampled**:	400 m <sup>-2</sup>				n.d.					
<i>Spathoderma clenchi</i>										
0-500	6	3	0	—	—	—	0	—	—	—
501-1000	2	6	0	—	—	—	0	—	—	—
1001-1500	3	4	1	19	6.3	19.1	0	—	—	—
1501-2000	1	14	1	6	6.0	—	1	2	0.1	2.9
2001-2500	5	45	5	579	115.8	125.1	14	417	9.3	154.0
2501-3000	6	23	0	—	—	—	10	342	14.9	102.4
3001-3500	1	6	1	1	1.0	—	1	10	1.7	9.8
3501-4000	7	5	0	—	—	—	0	—	—	—
4001-4500	1	43	0	—	—	—	0	—	—	—
4501-5000	22	28	0	—	—	—	0	—	—	—
>5000	4	0	0	—	—	—	—	—	—	—
Greatest density sampled**:	275 m <sup>-2</sup>				8 m <sup>-2</sup>					
<i>Chevroderma tumerae</i>										
0-500	6	3	0	—	—	—	0	—	—	—
501-1000	2	6	0	—	—	—	0	—	—	—
1001-1500	3	4	0	—	—	—	0	—	—	—
1501-2000	1	14	0	—	—	—	0	—	—	—
2001-2500	5	45	0	—	—	—	1	1	0.0	—
2501-3000	6	23	0	—	—	—	4	4	0.2	—
3001-3500	1	6	1	1	1.0	—	2	12	2.0	4.8
3501-4000	7	5	3	14	2.0	3.3	2	13	2.6	8.8
4001-4500	1	43	1	14	14.0	—	23	108	2.5	8.8
4501-5000	22	28	7	59	2.7	8.4	16	63	2.3	3.3
>5000	4	0	1	2	0.5	2.0	—	—	—	—
Greatest density sampled**:	8 m <sup>-2</sup>				24 m <sup>-2</sup>					

\* Sanders sled trawl, "Chalut à perche," Oban sled, and Wormley trawl.

\*\* Spade box corer, Birge-Ekman box corer.

teriorly in broken diagonals (Fig. 3Q). Mid-dorsally the spicules are arranged nearly parallel to the long axis of the body (Fig. 3S). Total body length averages 2.5 mm in one population; greatest length is 3.6 mm (Table VI). The broad trunk averages 0.6 mm and ranges up to 0.8 mm in diameter. The posterium is one-third total length, and broad, 0.3 mm average. Posterium length averages 0.8 mm, with posterium to trunk length index averaging 0.52 but ranging widely, from 0.38 to 1.14. The oral shield spicules are small and indistinct beside a medium-size oral shield (Fig. 3T).

Holotype: Total length 2.6 mm; trunk 1.6 by 0.7 mm; posterium 1.0 by 0.4 mm; index of posterium to trunk length 0.62. Oral shield 0.08 by 0.13 mm; index of oral shield to trunk diameter 1.49.

*Spicules.* Trunk spicules are very long and often narrow; a long, narrow blade tapers from a distinct waist to an acute or rounded apex (Figs. 5A, 11). The greatest thickness, up to  $9\ \mu\text{m}$ , is at the waist. Sides of the base are nearly parallel or slightly convex; the proximal end is usually triangular. The distinct or faint longitudinal groove seldom runs onto the blade. The blade is bent outward. Faint ridges often run along the base parallel to the longitudinal groove. The greatest length of the trunk spicules is nearly  $500\ \mu\text{m}$ . The trunk bears a few short, thin spicules with sharply pointed, short blades. Spicules from the ventral midline of the trunk are short, with a short blade and distinct waist (Fig. 11b<sub>2</sub>). Spicules from the posterium (*d*) are similar to those of the trunk. Oral shield spicules (*a*<sub>2</sub>) are similar to, but smaller than, those of

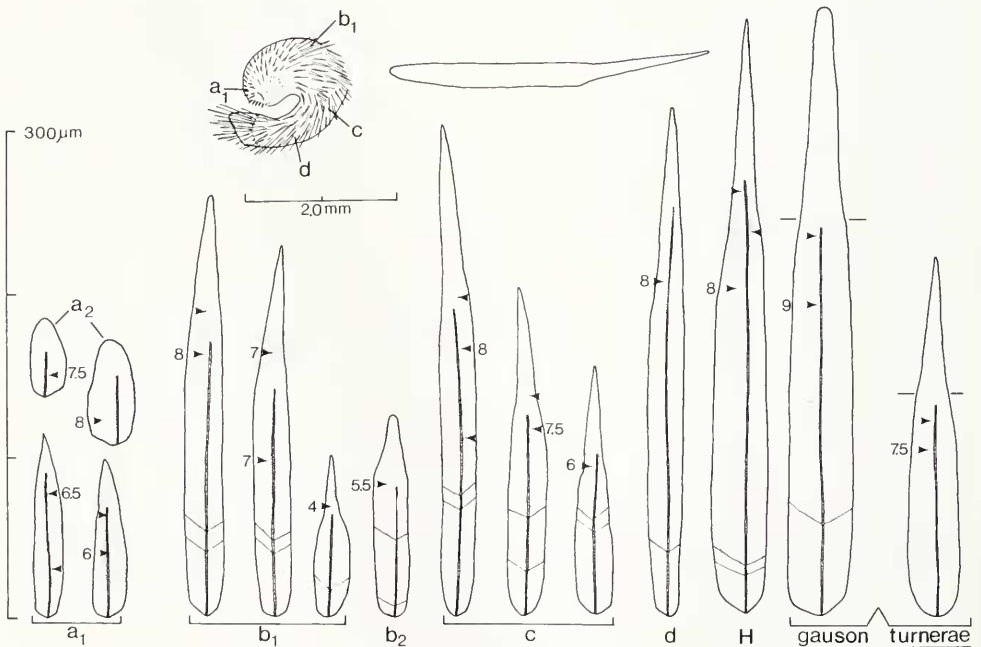


FIGURE 11. Spicules of *Chevroderma gauson* n. sp.: *a*<sub>1</sub>-*d* and specimen, paratype no. 1, 4426 m, West European Basin; oral shield spicules *a*<sub>2</sub> from paratype no. 2, 4632 m, West European Basin (type locality), and *b*<sub>2</sub> ventral trunk spicule from paratype no. 4, 4829 m, West European Basin; H, holotype, trunk spicule. Far right: spicules from specimens of *C. gauson* and *C. turnerae*, both of about average size, taken in the same sample at the type locality.

*C. turnerae*; spicules at the junction of anterium and trunk ( $a_1$ ) are similar in the two species.

*Radula*. The radula is typical for the family (Fig. 15  $g^1$ ,  $g^2$ ). The teeth are probably large, up to perhaps 130  $\mu\text{m}$ ; however, exact measurements were not made because the tips of the posterior teeth from the three radulae examined were brittle and broke off in preparation, and the four anterior pairs of teeth were worn. The jaws are long, up to 626  $\mu\text{m}$ , and up to 261  $\mu\text{m}$  wide. The central plate is long, up to 48  $\mu\text{m}$ , wide, up to 10  $\mu\text{m}$ , thick, and curved; it has a shallow groove running part or most of the length and the ends are blunt and rounded.

#### *Differentiation from C. turnerae*

*Chevroderma gauson* and *C. turnerae* were taken together in three out of the four stations where *C. gauson* occurred (Table I). Although the two species are distinctly different from each other in body shape where they co-occur, *C. gauson* is quite similar in shape to the short-tailed *C. turnerae* from the Argentine Basin continental slope and not significantly different from it in length or width of either trunk or posterium (Table VI). However, *C. gauson* is significantly different from all three *C. turnerae* populations analysed in the measure of posterium-to-trunk-length index ( $P < .05$ ).

Spicules of *C. gauson* and *C. turnerae* (Fig. 11, right) are distinguished primarily by length, relationship of greatest thickness to waist, and angle of blade to base, and secondarily by convexity of sides of the base, width of base and blade, shape of the proximal end, and distinctness of the waist. If they are visible in a specimen, the very large oral shield spicules of *C. turnerae* are distinctive.

The central plates distinguish the radulae of the two species (Fig. 15): in *C. turnerae*, but not *C. gauson*, the ends are tapered, and in *C. gauson*, but not *C. turnerae*, the plate is thick and bears a groove.

#### *Distribution*

*Chevroderma gauson* has been taken only at abyssal depths greater than 4400 m in the northern West European Basin north of 48°N (Table I; Fig. 1, squares). It was not taken in the abyss of the Iberian Basin just to the south (cruise ABYPLAINE, MNHN, Paris).

#### *Specimens examined*

The description is based on a total of 19 specimens from four stations.

#### *Chevroderma scalpellum* n. sp.

Figs. 1, 3U-W, 5C, 12, 15s; Tables I, VI

*Diagnosis*: Short, broad, translucent, less than 2½ mm long and up to 0.6 mm in diameter, posterium one-third total length; oral shield and oral shield spicules thin, small, and very indistinct; spicules with broad base, short, narrow blade, and distinct waist, with longitudinal groove not reaching proximal end of base, greatest length less than 300  $\mu\text{m}$ ; radula of moderate size, tooth length up to 106  $\mu\text{m}$ , jaw length up to 522  $\mu\text{m}$ , central plate long, 43  $\mu\text{m}$ , and narrow, 7  $\mu\text{m}$ , with blunt ends.

The species name means "a little scalpel."

Holotype: Angola Basin, 9°05'S, 12°17'E, 1427 m (ATLANTIS II-42 Sta. 202, 23/V/68). USNM No. 850231.

## Illustrated paratypes:

Nos. 1, 2: Type locality. USNM Nos. 850232 (No. 1), 850233 (No. 2).

No. 3: Cape Verde Basin, 10°30.0'N, 17°51.5'W, 1624 m (ATLANTIS II-31 Sta. 142, 5/II/67). USNM No. 850235.

## Description

**External morphology.** *Chevroderma scalpellum* is a very small, broad species averaging 1.5 mm in length and 0.4 mm in trunk diameter in one population (Table VI); the largest specimen is 2.4 mm long, and diameter ranges up to 0.6 mm. The posterium is broad, 0.3 mm on average, and one-third total body length, averaging 0.52 in posterium to trunk index; posterium length averages 0.5 mm and ranges from 0.3 to 0.8 mm. Mid-dorsally the spicules are arranged nearly parallel to the long axis of the body, but meet at a distinct angle where the trunk joins the posterium (Fig. 3W). The oral shield is small and indistinct with a thin cuticle; oral shield spicules are also small and indistinct (Fig. 3V).

**Holotype:** Total length 1.7 mm; trunk 1.2 by 0.5 mm; posterium 0.5 by 0.3 mm; index of posterium to trunk length 0.42. Oral shield 0.06 by 0.09 mm; index of oral shield to trunk diameter 1.08.

**Spicules.** The spicule base is broad relative to a usually short, narrow, often sharply pointed blade bent slightly outward; the waist is conspicuous (Figs. 5C, 12). Many spicules are nearly symmetrical. The longitudinal groove runs only part way along the base, not extending to the proximal edge but often extending onto the blade; it is sometimes nearly or totally lacking. The base may have faint, rather broad ridges and

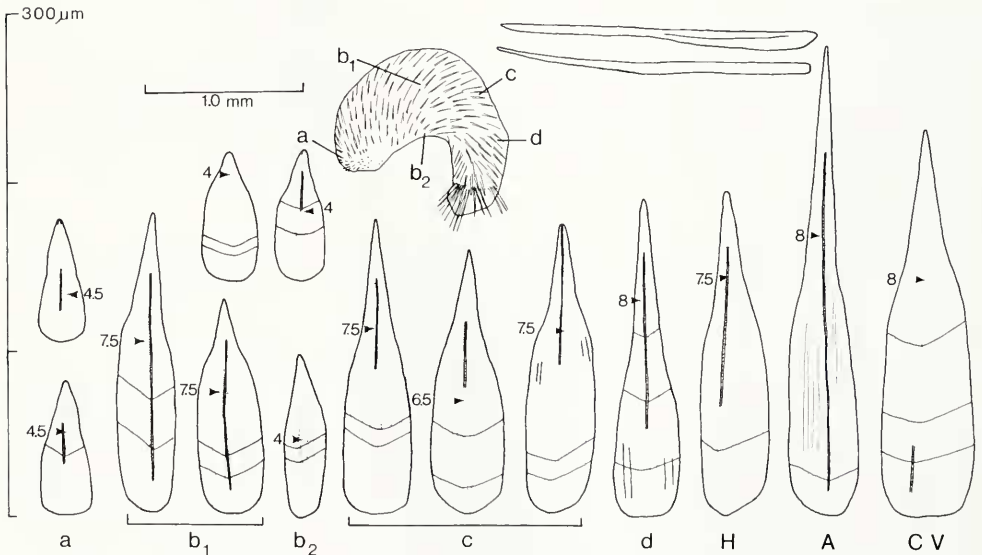


FIGURE 12. Spicules of *Chevroderma scalpellum* n. sp.: a-d and specimen, paratype no. 1, 1427 m, Angola Basin (type locality); H, holotype, trunk spicule; A, spicule from body region c of another specimen from type locality; CV, spicule from region c, paratype no. 3, 1624 m, Cape Verde Basin. Upper spicules: above, oblique view of body region c spicule; below, lateral view region d spicule; distal ends to left.

grooves; the sides of the base are straight to somewhat convex. Greatest thickness lies at the waist. Ventral spicules of the trunk (Fig. 12  $b_2$ ) are shorter than most other trunk spicules ( $b_1$ ) and are thickened further proximally. Spicules of the anterium ( $a$ ) have a broad base like those of the trunk. The bases of spicules from the posterium ( $d$ ) are the same length or shorter than those from the trunk, and the blades are bent further outward. Most spicules from trunk regions  $b$  and  $c$  of Angola Basin specimens are no longer than 225  $\mu\text{m}$ , but spicules from trunk region  $c$  in some specimens range up to nearly 300  $\mu\text{m}$  (Fig. 12A). Spicules from Cape Verde Basin specimens are larger, both broader and longer, than those from most of the Angola Basin specimens (Fig. 12CV).

*Radula*. The radula, examined from two specimens, is of moderate size for the family (Fig. 15s). Greatest tooth length is 106  $\mu\text{m}$ ; jaw length and width are up to 522 and 215  $\mu\text{m}$ , respectively. The central plate is long and narrow, up to 43  $\mu\text{m}$  long by 7  $\mu\text{m}$  wide, and has blunt, scarcely tapered ends.

#### *Differentiation from other Chevroderma species*

*Chevroderma scalpellum* is distinguished by its small size, indistinct oral shield, and spicules with their broad bases and short, narrow blades.

#### *Distribution*

*Chevroderma scalpellum* is an eastern Atlantic species found only in the Cape Verde and Angola Basins between about 10°N and 10°S over a narrow vertical range between 1427 and 2644 m (Table I; Fig. 1, hexagons).

#### *Specimens examined*

A total of 102 specimens from five samples was examined.

#### *Chevroderma whitlatchi* n. sp.

Figures 3H–K, 5E, 13, 15  $w^1$ ,  $w^2$ ; Tables II, VI

*Diagnosis*. Usually small, average length about 1.5 mm but up to 4.2 mm, with long posterium  $\frac{2}{5}$  total length; may have conspicuous translucent hump where trunk joins posterium; oral shield spicules small, distinct; spicules converge at angle along dorsal midline; trunk spicules with long base, distinct waist, and short, abruptly tapered, sharply pointed and broadly keeled blade, up to 200  $\mu\text{m}$  long; radula small, tooth with wing thickened and non-membranous, up to 100  $\mu\text{m}$  long, jaws up to 320  $\mu\text{m}$  long, central plate short with rounded ends.

This species is named for Dr. Robert B. Whitlatch, who gave me the Panama Basin material to examine.

Holotype: Panama Basin, 5°20.7'N, 81°56.2'W, 3912 m (ALVIN Dive 1239, Control 3, Core #2, 14/VII/82). USNM No. 850237.

#### *Illustrated paratypes:*

No. 1: Type locality (ALVIN 1232 Inj. BC #2). USNM No. 850238.

Nos. 2, 3: Aleutian Trench, 50°58.0'N, 171°37.5'W, 7298 m (SEVENTOW Leg 7, H-39, 20/VII/70). USNM Nos. 850240 (No. 2), 850241 (No. 3).



### Description

**External morphology.** *Chevroderma whitlatchi* is small and opaque; in many contracted specimens, the trunk is broadest posteriorly, producing a translucent hump at the juncture with the posterium. Spicules of the anterior half of the trunk, when it is contracted, assume an upright position; further posteriorly they meet at a distinct angle with the tips overlapped along the dorsal midline (Fig. 3H). They are arranged parallel to the body along the dorsal side of the posterium. Total length averages 1.5 and 1.6 mm in two populations (Table VI), with greatest length 4.2 mm. Trunk diameter averages 0.3 mm and ranges up to 0.6 mm. The posterium is long, two-fifths total length, and averages 0.6 mm in length by 0.2 mm in diameter, with greatest dimensions 2.1 and 0.3 mm, respectively; posterium to trunk length index averages 0.63 and 0.71 in the two populations, with a large range, 0.36 to 1.33. The two populations were not significantly different in any of five body measurements (Table VI). The oral shield spicules are small but distinct; the oral shield is large (Fig. 3K).

**Holotype:** Total length 2.7 mm; trunk 1.6 by 0.4 mm; posterium 1.1 by 0.3 mm; index of posterium to trunk 0.69. Oral shield 0.08 by 0.17 mm; index of oral shield to trunk diameter 3.40.

**Spicules:** The blade of trunk spicules is short relative to the base and narrow, abruptly tapering from a distinct waist to a usually pointed apex (Figs. 5E, 13c, H, A). The blade is bent outwards from the body wall and usually bears a medial ridge (juvenile) or distinct broad keel. The base is narrow and rotated about the long axis. The sides of the base are usually nearly straight and tapered proximally, so that the base is widest at the waist. Trunk spicules are thickest at, or just distal to, the waist. The longitudinal groove seldom extends beyond the base and may be very faint. Greatest spicule length is about 200  $\mu\text{m}$ . Spicules from the anterior trunk ( $a_1$ ) are wide; those from the ventral side of the trunk ( $b$ ) have a distinct waist. Spicules from the

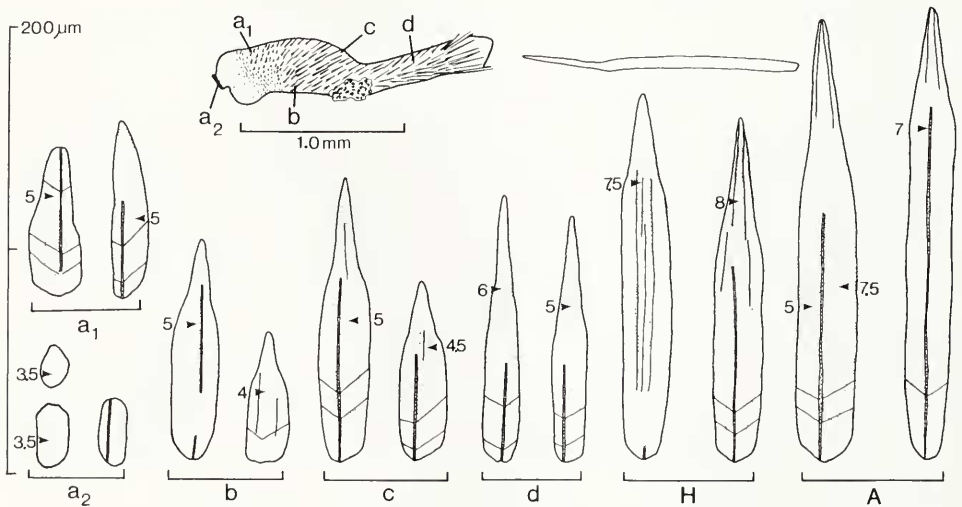


FIGURE 13. Spicules of *Chevroderma whitlatchi* n. sp.:  $a_1$ – $d$  and specimen, paratype no. 1, juvenile, 3912 m, Panama Basin (type locality); H, holotype, body region c; A, region c spicules from two specimens, 7298 m, Aleutian Trench, right spicule from paratype no. 3; above, lateral view, distal end to left, showing outward bend of blade.

posterium (*d*) have a narrower base and longer blade than those from the trunk. The oral shield spicules (*a*<sub>2</sub>) are small and thin.

*Radula*. The radula and jaws differ from other species of *Chevroderma* in their smaller size; in the thickened, twisted base of the jaws; in the serrations of the brush membrane, which are either very thin or lacking (although present in juvenile specimens); and in the thickened, non-membranous tooth wing (Fig. 15w<sup>1</sup>, w<sup>2</sup>). In four specimens examined, tooth length was 110 μm in a large specimen 3.3 mm long and jaw length and width 429 μm and 157 μm, respectively; in specimens of average length, tooth length is about 70 μm and jaw length and width range up to 320 and 110 μm, respectively. The central plate is short, up to 27 μm, and 5 to 7 μm wide, with usually rounded, untapered ends.

### Distribution

*Chevroderma whitlatchi* is an abyssal and hadal species taken in the central and eastern North Pacific. It occurs at high densities in the soupy muds of the Panama Basin and Aleutian Trench. Like *C. turnerae*, it covers a great depth range, from

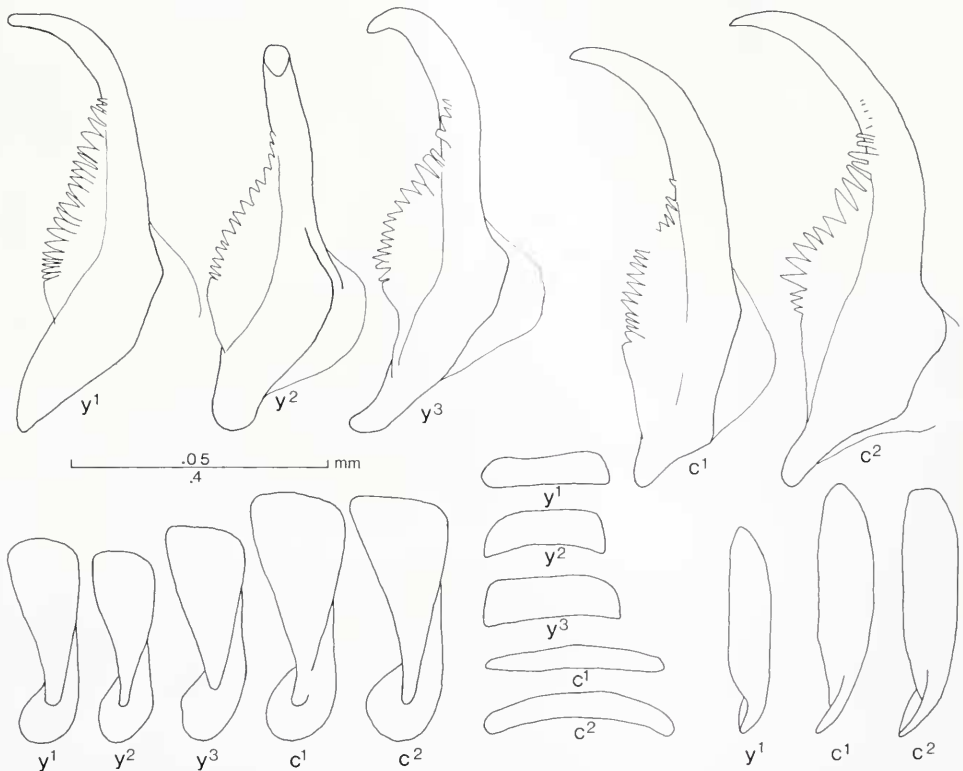


FIGURE 14. Radula teeth, central plates and jaws of *Prochaetoderma yongei* n. sp. and *Spathoderma clenchi* n.g. n. sp. *y* = *P. yongei*: *y*<sup>1</sup> paratype no. 1, 1470 m, North American Basin (type locality); *y*<sup>2</sup> paratype no. 3, 805 m, North American Basin; *y*<sup>3</sup> paratype no. 2, 1546 m, Namibia Basin; *c* = *S. clenchi*: *c*<sup>1</sup> paratype no. 2, 2178 m, North American Basin (type locality); *c*<sup>2</sup> paratype no. 4, 2897 m, West European Basin. Scale equals 0.05 mm for teeth and central plates and 0.4 mm for jaws.

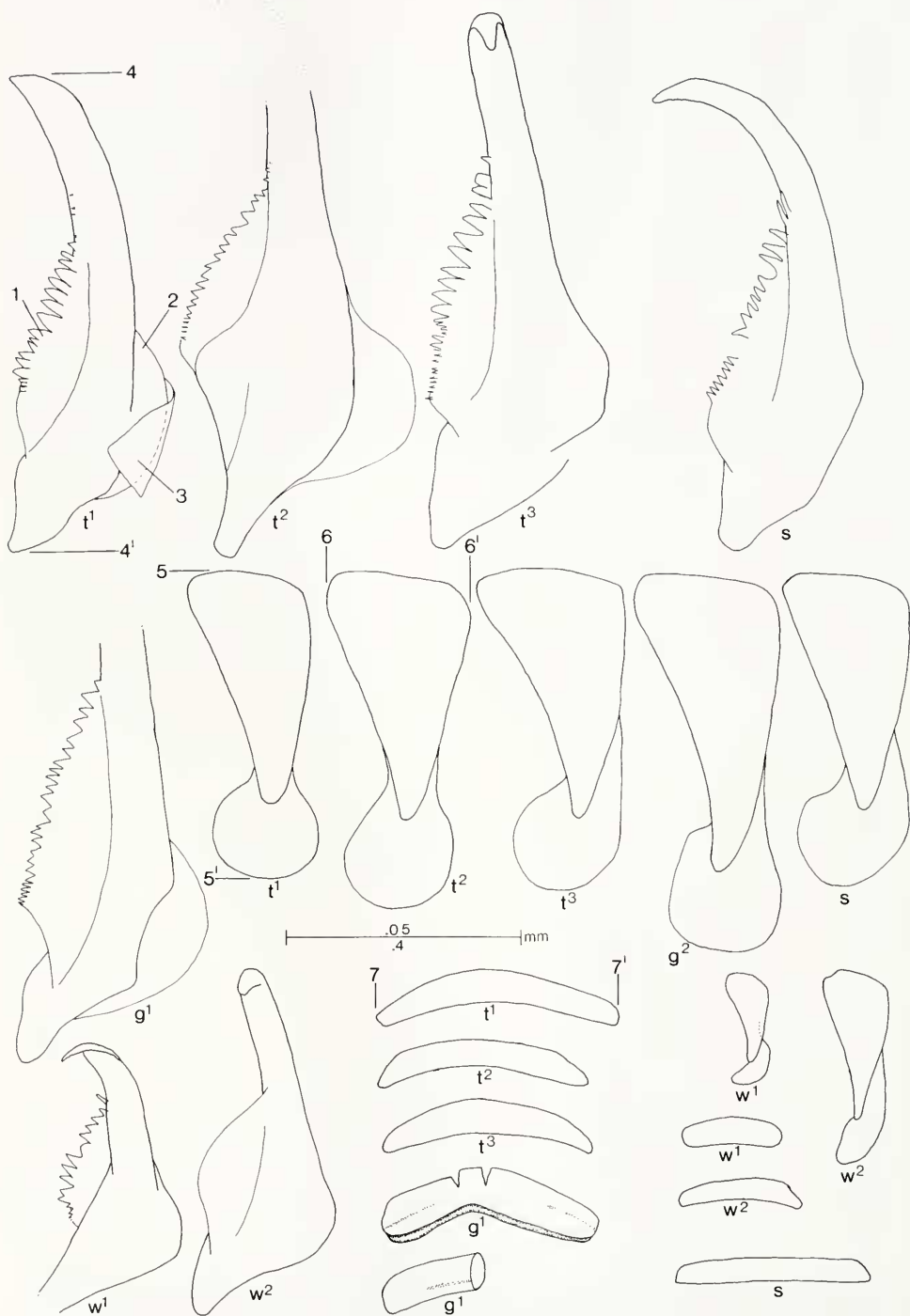


FIGURE 15. Radula teeth, central plates and jaws of *Chevroderma* (n.g.) species. *t* = *C. turnerae* n. sp.: *t*<sup>1</sup> paratype no. 3, 4833 m, North American Basin (type locality); *t*<sup>2</sup> specimen from 3305 m, Argentine Basin (All-60 Sta. 259); *t*<sup>3</sup> paratype no. 2, 3797 m, Angola Basin; *s* = *C. scalpellum* n. sp.: paratype no. 2.

2800 m off Oregon and 2727 m near the Galapagos Rift to over 5000 m in the mid-Pacific and over 7000 m in the Aleutian Trench.

About 90 percent of the specimens in box core samples from the Aleutian Trench and Panama Basin occurred within the upper 2 to 3 cm of sediment; the remaining 10 percent were below this level.

#### *Material examined*

Sixty-eight specimens were examined, 62 of them from the Panama Basin and Aleutian Trench, the remaining 6 scattered among 4 locations (Table II).

### DISCUSSION

#### *Taxonomic characters*

The dependence on spicule morphology for delimiting species and genera in the Prochaetodermatidae is based on ease of use, accessibility of the character, and biological considerations. Spicules and the cuticle in which they are embedded probably not only serve as a protective cover, but also—and perhaps primarily—as antagonists to muscle activity during locomotion. They also may adapt the animals to particular horizons within the sediment. Very small differences between species in body wall musculature, which would be very difficult to determine histologically, can be expected to be magnified in the morphology of the spicules. Body wall musculature, and thus spicule morphology, is considered to be a conservative character.

The body measurements of preserved, contracted specimens, although not descriptive of living animals, are related to the arrangement of internal organs and body wall musculature and allow for statistical analysis not readily possible with spicules, which vary greatly in size within a single specimen. As most identifications of deep-sea Aplacophora will be of preserved specimens, body measurements should be of continuing usefulness.

The variability in taxonomic characters described here and interpreted as belonging to single species may actually be due to the existence of sibling species living in different basins, but there is neither sufficient knowledge about the reproductive biology of these animals nor adequate samples on which to base judgements. It has seemed most sensible to treat apparently minor character differences between specimens from different ocean basins as variations within a species, rather than naming species according to their locality, *i.e.*, by ocean basins. A like situation in the protobranch family Malletiidae has recently been treated in a similar manner (Sanders and Allen, in press).

#### *Distribution*

*Geographic.* Vertical depth distribution and horizontal geographic range are directly related to one another in the Prochaetodermatidae. Three of the five Atlantic species described here—*Prochaetoderma yongei*, *Spathoderma clenchi*, and *Chevroderma turnerae*—have vertical depth ranges greater than 1500 m; all three are ampho-Atlantic

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1427 m, Angola Basin (type locality); g = *C. gauson* n. sp.; g<sup>1</sup> specimen from 4632 m, West European Basin (type locality); g<sup>2</sup> paratype no. 1, 4426 m, West European Basin; w = *C. whitlatchi*; w<sup>1</sup> paratype no. 1, 3912 m, Panama Basin (type locality); w<sup>2</sup> specimen from 7298 m, Aleutian Trench (SEVENTOW Leg 7 Sta. H-39). 1 membranous serrated brush, 2 membranous wing, 3 lateral toothlike projection of radula membrane, 4-4' tooth length, 5-5' jaw length, 6-6' jaw width, 7-7' central plate length. Scale = 0.05 mm for teeth and central plates, 0.4 mm for jaws.

and have been taken from four or more ocean basins (Fig. 1, Table I). One, *C. turnerae*, is an abyssal species; both *P. yongei* and *S. clenchi* are continental slope species that do not extend into the abyss below 3300 m. *Chevroderma scalpellum* and *C. gausson* have both restricted depth ranges and geographic distributions; the former, with a depth range of 1217 m, is restricted to two adjacent ocean basins, and the latter, with a depth range of 403 m, occurs only in the northern West European Basin.

Such a correspondence in range of vertical and horizontal distribution is not unique to the Prochaetodermatidae and is considered to be at least in part due to mode of development and dispersal ability (R. Scheltema, 1972; Sanders, 1977). For an example, the protobranch bivalves are a molluscan group similar to the Aplacophora in development insofar as it is known for the two groups; either a lecithotrophic larva develops within a ciliated, cellular test or development is direct. A compilation from studies on 27 protobranch species in six families or subfamilies in the Atlantic (Allen and Sanders, 1973, 1982; Sanders and Allen, 1973, 1977, in press) shows that fourteen protobranch species have vertical depth ranges less than 1500 m; all but one of these are restricted to one or two ocean basins and to one side of the Atlantic. The remaining 13 species have depth ranges greater than 1500 m and are all amphi-Atlantic or occur in more than one ocean; but unlike the Prochaetodermatidae with large depth ranges, all 13 extend into the abyss below 3300 m.

R. Scheltema (1972, Table II) showed that two out of seven species of the protobranch genus *Nucula* in the northwest Atlantic were abyssal and had depth ranges greater than 1500 m, geographic ranges in three amphi-Atlantic basins, and lecithotrophic development. In one species, however, a lecithotrophic larval stage was related to a restricted depth range (less than 1000 m) and a geographic range of only two amphi-Atlantic basins, so factors other than mode of development determine distribution. A detailed study of reproduction and development in the species of Prochaetodermatidae described here has not yet been made.

Species with a dispersal ability are assumed to be better able to become widespread in the continuous abyss than on the continental slopes. However, both *P. yongei* and *S. clenchi* are broadly distributed geographically despite their restriction to less than 2178 and 3356 m, respectively, although in the western Atlantic they do not breach the partial zoogeographic barrier at 34°N and are restricted to the North American Basin, probably because of slope currents (Cutler, 1975). The abyssal *C. turnerae*, on the other hand, is ubiquitous throughout Atlantic basins, apparently missing only in the Iberian and Guyana Basins, the latter faunally unique for many taxa. The Pacific Ocean species *C. whitlatchi*, like *C. turnerae*, has both a very large depth distribution, extending from 2727 m to hadal depths over 7000 m, and a broad geographic range (Table II). The question arises, Why is the other abyssal *Chevroderma* species, *C. gausson*, so restricted in range? Does it have a different dispersal ability, or ecological requirements met only by the northern West European Basin?

*Distribution within ocean basins.* Only a few data exist on local abundances within a basin, and only for the North American and West European Basins in the Atlantic. From grabs and box cores come quantitative data on density of species as number per square meter and their rank order. From sled trawls come data on total numbers of individuals by species or higher taxa and their percent composition and rank order. For the Pacific, there are data from one ¼-m<sup>2</sup> box core taken in the Aleutian Trench, two ¼-m<sup>2</sup> box cores from the mid-Pacific, and fifteen 225 cm<sup>2</sup> box cores in the Panama Basin. Based on either percent of total individuals or on density per square meter, the data show that particular species of Prochaetodermatidae are numerically an important part of the fauna at certain localities in the North American Basin and eastern Pacific, but not in the West European Basin or mid-Pacific.



In the North American Basin, species diversity in the Prochaetodermatidae is low, only three species, but numbers of individuals may be very high locally for two of them: up to 400 m<sup>-2</sup> for *Prochaetoderma yongei*, with 200 m<sup>-2</sup> not uncommon, and up to 275 m<sup>-2</sup> for *Spathoderma clenchi*, with over 100 m<sup>-2</sup> not uncommon (G. T. Rowe, unpub. data). Expressed either in numerical rank order or as a percent of total fauna, *P. yongei* ranks first at depths of about 1760 m at 39°46'N, 70°37'W and constitutes more than 6 percent of the fauna [Grassle, 1977, Table 2, *Prochaetoderma* sp. (abundance recalculated here); see also Table I, this paper: OCEANUS-10 Sta. 367, 370]. In a sled trawl sample near the same location, 911 *P. yongei* formed 3.6 percent of the total fauna (Table I: ATLANTIS II-12 Sta. 73; Hessler and Sanders, 1967, Table 3). Similarly, at somewhat greater depths between 2351 and 2673 m, *S. clenchi* ranked third in species abundance and formed 5.4 percent of the fauna (Rowe *et al.*, 1982, Table 2, *Prochaetoderma* sp. A; data are lumped from samples taken at several localities).

In the West European Basin the Prochaetodermatidae are represented by at least eight species, including those from the North American Basin (Scheltema, 1985). Although the diversity is greater than in the North American Basin, the numerical abundance of two species is lower: *P. yongei*, for which quantitative data are lacking, was taken only occasionally in sled trawls in low numbers and comprised only 0.07 percent or less of all individuals; *S. clenchi* formed at the most only 0.2 percent of the fauna, and in the Bay of Biscay, greatest densities were low, 8 m<sup>-2</sup>.

*Chevroderma turnerae* occurred in low densities throughout its range, with not more than 75 individuals taken in a single sled trawl and densities ranging from 8 m<sup>-2</sup> in the North Atlantic Basin to 24 m<sup>-2</sup> in the Bay of Biscay (Table I: OCEANUS-10 Sta. 353; BIOGAS XI KG-207).

Data from nonquantitative sled trawls for *P. yongei*, *S. clenchi*, and *C. turnerae* show similar vertical distribution patterns within the two north Atlantic basins, but, like data from quantitative gear, uneven abundances in the two slopes species. The number of sled trawl samples from all cruises are given for each basin by 500 m depth intervals in Table VII (N). (All western Atlantic samples were taken with a Sanders sled trawl; data for the West European Basin are based on samples from four types of sleds and trawls. Replicates taken on CENTOB cruises BIOGAS VI and INCAL sampled the aplacophoran fauna equally efficiently.) For each species, the number of samples in which it occurred at each depth zone was tabulated and the individuals in these samples summed ( $\Sigma X$ ; data from Table I). From these data the average number of individuals per sample was computed for each 500 m interval ( $\bar{X} = \Sigma X/N$ ).

All three species are most numerous in their mid-ranges, *P. yongei* and *S. clenchi* most markedly so in the North American Basin, where these two species are not only abundant, but also common, occurring in most trawl samples taken at their mid-ranges. The same species are less commonly found in the West European Basin, where they occurred in fewer than one-half the samples at all depths, and less abundant in individual samples, with 10 to one hundred-fold fewer individuals per sample. *Chevroderma turnerae* has low mean numbers of individuals per sample but is more evenly distributed across the ocean than either *P. yongei* or *S. clenchi*, occurring in about one-third of all samples in both basins.

The high variance-to-mean ratios ( $s_{\bar{x}}^2/\bar{X}$ ) indicate a patchy distribution in both basins for all three species, as indicated also by the absolute sample sizes in Table I.

The Pacific species *C. whitlatchi* is very abundant in both the Panama Basin, where it ranges up to 178 m<sup>-2</sup>, and in the Aleutian Trench, with 124 m<sup>-2</sup>; at the latter location it ranked second in species abundance (Jumars and Hessler, 1976; Hessler, unpub.). In four other localities, however, total numbers taken were only 1 or 2.

*Importance of Aplacophora in the deep sea fauna*

The Aplacophora are usually considered an insignificant part of the faunas in which they are found. Certainly the class is small in species numbers compared to other higher taxa in the deep-sea, *i.e.*, polychaetes, bivalves, crustaceans, and nematodes. It is, however, the individuals of species that interact, and certain species of Aplacophora therefore may have an important role in a community. Although the total polychaetes or bivalves present at a particular locality may outnumber the Aplacophora, a single aplacophoran species (*e.g.*, *Prochaetoderma yongei* or *Chevroderma whitlatchi*) nonetheless may be among the most abundant species present. The Prochaetodermatidae are thought to be omnivores that feed on a wide variety of organic material, probably living and dead (Scheltema, 1981), a feeding habit that equips them well, and perhaps better than most other species, to live in an environment where food may be limiting.

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